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Morden-Smithsonian Expedition
to Dominica:
The Lichens (Graphidaceae)

MICHAEL WIRTH
and
MASON E. HALE, JR.



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ABSTRACT

Wirth, M., and Mason E. Hale, Jr. Morden-Smithsonian Expedition to Dominica: The Lichens (Graphidaceae). *Smithsonian Contributions to Botany*, number 40, 64 pages, 23 figures, 1978.—The four main genera of the Graphidaceae in Dominica, *Graphis* (27 species), *Phaeographis* (7 species), *Graphina* (25 species), and *Phaeographina* (6 species), are treated monographically with full synonymy, descriptions, chemistry, and illustrations. The family as a whole is common in all primary and secondary forests and at all elevations. Eight new species are described: *Graphis imshaugii*, *G. isidiifera*, *Phaeographis mordenii*, *Graphina carneoviridis*, *G. suberythrella*, *G. triphoroides*, *Phaeographina atrovermicularis*, and *P. coriaria*. Three new combinations, *Graphina columbina* (Tuckerman) Wirth and Hale, *G. illinata* (Eschweiler) Wirth and Hale, and *G. plurispora* (Redinger) Wirth and Hale, are also made.

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Introduction

This study is a continuation of a floristic treatment of the lichen flora of Dominica. The first article on the Parmeliaceae (Hale, 1971) and a second on the Thelotremataceae (Hale, 1974) should be consulted for general information on the geography and ecology of the island. The specimens examined in this study came from four sources: the historical collections of Elliott (preserved in BM and TUR) and the more recent materials of Hale (US), Imshaug (MSC), and Wirth (US). A variety of localities and habitats was visited by each collector, although Hale worked primarily in the higher elevation rain forest that was being logged 1968–1972, and Imshaug and Wirth studied both the high mountain tops and lower, disturbed forests. While we do not claim that all of the Graphidaceae have been discovered, this treatment must include a high percentage of the graphidaceous flora of Dominica.

We owe special thanks to Mrs. William J. Morden, who generously supported field and herbarium studies by Hale. Dr. Henry Imshaug very kindly placed his collections at our disposal. We are also indebted to Dr. Minoru Nakanishi for the use of his unpublished data and keys for many of the Asian

species. Finally, we thank curators of the herbaria and institutions who so promptly sent specimens on loans, in particular Dr. Teuvo Ahti (H), Dr. Reino Alava (TUR), and Mr. Peter James (BM).

Generic Delimitation

The delimitation of the Graphidaceae is still a matter of difficulty. Most lichenologists now reject from the family all those groups that have obviously branched paraphyses, globular asci with a bitunicate nassasceous structure, and cylindrical spore locules. Thus, *Chiodecton*, *Opegrapha*, *Arthonia*, and their segregate genera are generally excluded from the Graphidaceae sensu stricto. *Melaspilea* also seems best excluded; even though the paraphyses frequently appear free and unbranched and the two-loculed spores are shared by a few *Graphis* species, the structure of the asci in *Melaspilea* seems quite dissimilar to that of *Graphis*.

Using the criteria above, one is left with a group of four closely related genera without stroma-like tissue (*Graphis*, *Phaeographis*, *Graphina*, *Phaeographina*), four parallel genera with such tissue (*Glyphis*, *Sarcographa*, *Medusulina*, *Sarcographina*), and a number of minor genera whose relationships are unclear (*Helminthocarpon*, *Aulaxina*, *Gyrostomum*, etc.). Although it is customary to refer to these major genera as ascohymenial, even that seems to be in doubt (cf. Groenhart, 1965:4). We have, in any case, continued the ascohymenial terminology

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usually applied to the family, using the terms "hymenium" and "paraphyses" without necessarily accepting them as ontogenetically correct.

To a great extent, all genera (in phanerogams as well as in lichens) are artificial constructs, in that no fixed criteria exist for delimiting any taxa above the biological species. In groups where cytogenetics, breeding experiments, etc., can reveal something of the direction of evolution, genera may in fact be an approximation of biological (i.e. evolutionary) relatedness. Obviously, in the crustose lichens, such information is mostly lacking. In addition, ontogenetic studies of lichen reproductive structures are scarce and frequently open to different interpretations; for example: What exactly is a hymenium? Is the structure of the ascus of great importance, or little?—and so on.

In the light of such uncertainty, a reasonable approach seems to be the recognition of genera on practical grounds, so that at least problems of identification and curating are more manageable. On such grounds, the major genera of the Graphidaceae are reasonably delimited. By using spore septation and color as primary criteria, and the development of stroma-like tissue as a secondary criterion, one can distinguish the major genera of the family with relative ease.

To be sure, specimens (and species) exist that bridge the gap between these form genera and tend to blur the distinctions. In *Graphina vestitoides*, for example, only the end locules of otherwise typical *Graphis* spores become longitudinally divided. Many of the very small-spored *Graphina* species (*G. insignis*, *G. colliculosa*, etc.) have barely muriform spores which, when not quite mature, will resemble four-loculed *Graphis* spores. The problems of spore color and septation in such borderline species as *Graphina acharii* and *Phaeographina chrysocarpa* have been mentioned elsewhere (Wirth and Hale, 1963).

Intermediate states also exist between the stromatoid and nonstromatoid genera. A fine example can be seen in many specimens of *Phaeographis exaltata*, which frequently show, in portions of a single thallus, characteristics of both *Phaeographis* and *Sarcographa*.

There is, however, a more serious objection to spore genera. One can regard a genus as consisting of species that share a large number of characteristics in common; this approach, common among

"numerical" taxonomists, assumes that "relatedness" in the biological sense frequently can be approximated by measuring the over-all similarity of taxa. As there are few (if any) good biological criteria for genera in crustose lichens, this approach may be quite useful. One can find many examples of species that are extremely similar but are presently placed in different genera only because of a difference in spore color and/or septation. We will call such forms "sporomorphs," defined as follows: two or more species that are extremely similar (or identical) in external morphology, anatomy, chemistry, and spore size, as far as we can determine with present techniques, but that are presently placed in different genera on the basis of spore septation and/or spore color only.

Sporomorphs are common in the Graphidaceae; good examples occurring at least in part in Dominica are *Phaeographis arthonioides*/*Graphis humilis* and *Graphina incrustans*/*Graphis dumastii*.

The existence of sporomorphs casts considerable doubt on the ability of spore features to establish genera of closely related (i.e. very similar over-all) species. Is it possible, for example, that the muriform condition simply represents a later ontogenetic stage of the *Graphis* spore that has become genetically fixed? If such were the case (and indeed all muriform spores seem to go through a *Graphis*-like juvenile stage), then *Graphina incrustans* may be a recent descendant of *Graphis dumastii*, and these two species should be regarded as closely related. Placing these species in different genera, while grouping *G. incrustans* with otherwise very dissimilar *Graphina* species, would then be illogical.

If this objection to spore-based genera is accepted, then one is faced with a considerable problem of nomenclature. Ignoring the spore color and septation as major generic criteria, then only two choices appear to be acceptable. One choice would be the erection of scores of segregate genera based on over-all similarity of exciple structure and chemistry. It is not apparent to us how much such a system could be established or used without the help of a computer. The second generic approach would be to reduce all the spore-based genera back into *Graphis*. Such a system, which may be biologically quite acceptable, would raise immense practical problems; there are simply too many species of Graphidaceae (over one thousand) to be handled conveniently.

In light of these practical problems, we have chosen to accept the major spore-based genera for the Graphidaceae. Whenever possible, however, we have indicated similar species and sporomorphs, regardless of present generic lines.

Species Delimitation

With essentially no knowledge of speciation in the Graphidaceae, we have had to use the traditional approach of concentrating on discontinuities of morphology, anatomy, chemistry, and size. This approach works best with large collections of specimens; unfortunately, in the Graphidaceae, as in other tropical crustose groups, one is too often accomplishing no more than cataloguing types. In light of this problem we have elected to maintain a very narrow species concept, leaving "lumping" to some future monographer blessed with abundant collections.

SPORES.—Several features associated with spores supply useful means of separating species. In a family with such a large range of spore size (6 μm to 300 μm), it is not surprising to find discontinuities of size classes. We have, whenever possible, maintained species on this basis. Within a given individual, however, spore size commonly varies by a factor of 1.5 to 2; with additional collections, many of the species presently maintained primarily on spore size may vanish, while in other cases more species will be described.

A second spore character of considerable interest is number per ascus. In many specimens, this number remains quite constant, and can be used as a species criterion. A good example is *Graphina chlorocarpa* and *G. balbisii*; individuals with one spore per ascus are assigned to *G. chlorocarpa* and all others to *G. balbisii*. Unfortunately, the spore number is quite variable in other species; *Graphina virginea* commonly will have 2, 4, 6, or 8 spores per ascus in the same thallus. Only larger population samples, when they become available, can help us solve this problem.

The number of locules per spore, though roughly correlated with spore size, may be useful where only four locules per spore occur. This condition seems constant, and we have accepted species (particularly in *Phaeographis*) where the main, and perhaps only, distinction consists of four versus more than four locules per spore.

HYMENIUM.—Although hymenial character-states supply much useful information, we have seen very few cases where species are established primarily on hymenial features. One such feature is the presence of droplets or inclusions in the hymenium; it is not yet clear if these inspersiones are a constant feature within a species or not. At least one species has been based primarily on these inclusions (*Graphis inspersa* Redinger (1935)). It should be noted that the droplets or particles disappear in Hoyer's medium, and hence must be looked for in water mounts.

In all the descriptions given here, hymenium height is stated. We have found this measurement to be a very useful single feature to indicate gross apothecium size. In species with very heavily carbonized exciples the hymenium height becomes proportionally small; for most other species, it is an excellent indicator of over-all size. Hymenial measurements include the epilhymenium ("epithecium" of older literature), which is frequently darkened.

EXCIPLE.—Exciple characters have traditionally formed the backbone of species delimitation in Graphidaceae. In addition, almost all subgeneric taxa are based on excipular characters (see Redinger, 1933:4 and 1935:2). Many of these characters now appear to be quite variable and unreliable. In the discussion below, it should be emphasized that all observations were made from very thin hand sections, mounted in Hoyer's medium, and briefly boiled to drive out air. Without this approach, it is very difficult to determine accurately excipular structure. Occasionally, three to four days must elapse after mounting a section before all minute air bubbles disappear; when present, they may mimic carbonization very closely, particularly in the labial tips of totally uncarbonized exciples.

Exciple Carbonization: Carbonization is not an all-or-nothing proposition. Many ascocarps will show heavy carbonization in portions of a thallus and only partial or slight blackening in others. We have maintained several species on the basis of incomplete vs. complete carbonization of the lateral exciple walls, but more abundant collections may force such taxa into synonymy.

One odd variant of carbonization appears in some graphids. The bases of the exciples are connected by a more or less continuous black to brown (partially carbonized) band. Such a condition appears commonly in *Graphina insignis*, and less fre-

quently in *G. virginea* and *G. confluens*. We have found no correlation with any other features; in fact, the black band may be quite absent in parts of a thallus and present elsewhere.

Many species of Graphidaceae lack carbonization completely. In some of these, the exciple itself seems to be non-existent. In many of the fissurine *Graphis* species (i.e., those with fissure-like apothecia in surface view, and four-locular spores), the term "exciple" may be inapplicable, as the hymenium would seem to be bounded by unmodified hyphae; in many of these, what appear to be excipular labia are, in fact, masses of bark cells. It may well be that presence of large amounts of bark laterally bounding the hymenium is significant as an indicator of endophloeodal development of the ascocarp.

Open vs. Closed Exciples: In many specimens with carbonized exciples, all sections from a thallus will be consistently open (or consistently closed) below, but many others will vary from completely open to completely closed within the same thallus. The weight commonly placed on this character-state to establish species, subgenera, or sections is unjustified. When no carbonization exists, it becomes even more difficult to determine if closure is present, even in a single transverse section. It seems likely that many species presently separated only by excipular closure will prove synonymous with more collections.

In addition, it may well be that degree of basal carbonization, and hence the overall height of the ascocarp above the thallus, is a function of age. This possibility is discussed more fully below.

Labial Striae: Another character on which much emphasis has been placed, probably incorrectly, is the absence, presence, and degree of striation in the labia. Two basic types of striae occur in the Graphids and must be treated separately.

In the first type, occurring in both carbonized and clear exciples, the surface of the lips is obviously indented, forming distinct longitudinal grooves. This character is usually quite variable within a single thallus; maintaining species on degree of striation must be regarded with great suspicion. In fact, many specimens with no striations on the majority of apothecia can be found to have them on a few. Many species-pairs can be found in the family where the members are distinguished only by presence or absence of longitudinal striae (see,

for example, *Graphis anguilliformis* and *G. flexibilis*).

It is possible that the striations in both carbonized and clear exciples may be a function of age. Specimens that have high ascocarps with thick bases and (frequently) disintegrating hymenia (all presumed to be signs of age) also usually have many striae. On the same thallus one can occasionally find low ascocarps with less basal carbonization and vigorous (fertile) hymenia; these structures are frequently associated with fewer (sometimes no) labial striae. In addition, in species with both clear and carbonized exciples, new hymenia arise below old ones; this phenomenon, which may be seasonal, apparently ruptures the excipular tissue below the old hymenium, and compresses it into new lateral striae. This phenomenon has been pointed out earlier for carbonized species (Redinger, 1935:98). In uncarbonized forms, an increase in the number of internal striae (described below) occurs; we have seen it very frequently in sterile Mexican material of cf. *Graphina peplophora* (Figure 1). If this interpretation is correct, then the number of striae per ascocarp would increase seasonally (at least in these species), and hence would be useless taxonomically.

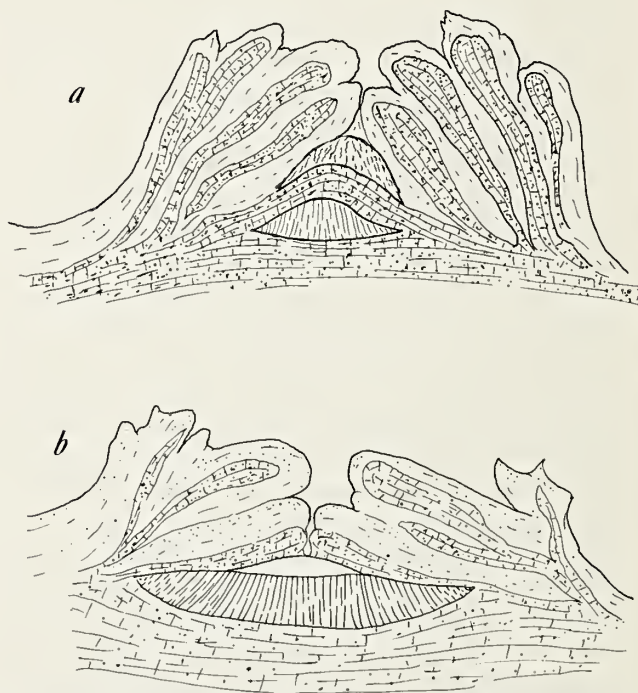


FIGURE 1.—Cross sections of *Graphina peplophora* from Mexico: a, Wirth 150; b, Wirth 361.

The second major type of striae occurs only in uncarbonized exciples. What appear to be dentations or striae occur within the labial tissue, without any trace of surface grooves. Examination of many ascocarps on large thalli reveals that these striations arise with age, apparently by lateral portions of the hymenium compacting, darkening, and being incorporated into the lateral tissue surrounding the hymenium. Along with these compactations, the portion of the exciple below the hymenium thickens and raises the whole ascocarp farther from the thallus surface. Thus, a single specimen may have low ascocarps with entire lips and an open exciple and high ascocarps with massive bases and (internally) striate labia. The cross sections of *Graphina colliculosa* exciples (Figures 8f,g; 9a) illustrate these conditions well.

Labial Convergence: The degree of convergence of labial apices, commonly used to separate species and subgenera, is also beset with problems.

One common occurrence is the rapid spreading of otherwise convergent labia of carbonized exciples as soon as a moistened ascocarp is sectioned. Such species as *Graphis candidissima* Zahlbruckner and *G. subamylacea* Zahlbruckner will appear to belong to Section *Phanerographa* (intact, spreading carbonized lips) when in fact the spreading is an artifact caused by the hymenium swelling rapidly.

A more serious problem arises in many species with uncarbonized exciples. In *Phaeographis albida* (Figures 7a,b) and *Graphina colliculosa* (Figures 8f,g; 9a), ascocarps with convergent labia (no disc visible) and divergent labia (prominent disc visible) may occur on the same thallus. If the two forms occur on different specimens, the surface appearance will differ strikingly and result in the description of two species.

THALLUS.—Very few character-states of importance are derived from the thallus. Color, in general, is not a practical feature, with the possible exception of those endophloeodal thalli which frequently signal this condition by a distinctive yellow-brown shade.

The thalli of some species show a distinct prosoplectenchymatous upper layer. The hyphae seem to align perpendicularly to the ascocarps, and hence cross-sections of the lirellae almost always exhibit characteristic parallel filaments. This condition seems to be consistent within species, and may prove useful in distinguishing members of certain

species complexes (see, particularly, the *Graphis triticea* group).

Very few species of Graphidaceae show highly pronounced surface features such as soredia or isidia. More subtle aspects of texture may be constant enough for systematic purposes, as in thalli with pronounced glossy or powdery surfaces. A lower cortex is lacking in the family, with the exception of the extremely odd *Graphis coriacea* Vainio from Guadeloupe.

In all cases, we have found the algal constituents of no use for species level distinctions.

CHEMISTRY.—*The Iodine Reaction:* In most species of Graphidaceae, water squashes of mature spores react with almost any concentration of iodine solution and rapidly turn a deep blue-violet. The hymenium in most species is iodine negative, i.e., absorbs the solution and turns yellow-orange, but never violet. Within a species the reactions seem to be quite constant; see *Phaeographis albida* for the one exception known to date.

Many of the “fissurine” *Graphis* species, and many species of *Phaeographis*, have spores that are iodine negative, or oddly and slowly I positive (turning red-purple). In a few species (*Graphina virginea*, *G. diorygmatoidea* (Vainio) Zahlbruckner, *G. confluens* (Fée) Mueller Argoviensis, *Phaeographis albida*), the entire hymenium, or at least the epihymenium, turns bright violet with iodine. The reaction seems constant enough to make it very useful in species identification. It is unclear as to what compounds are involved in the reaction.

Lichen Acids and Other Compounds: In general, we have tried to erect and maintain species that are chemically homogeneous (for exceptions, see *Phaeographis exaltata* and *Graphina platyleuca*). In many cases, this has meant maintaining species pairs (or triplets) entirely on chemical grounds. It would appear that the Graphidaceae will have many cases where a series of morphologically identical species are separable only by the presence or absence of stictic and/or norstictic acids.

Recent chemical testing shows that more than half of the species in the Graphidaceae are TLC negative, in other words lacking any phenolic secondary products. The most common lichen substance in the TLC positive remainder is unquestionably norstictic acid. Fairly abundant, though not common, are stictic acid and the “quintaria” unknowns. Very uncommon are psoromic, lecanoric,

protocetraric, salazinic acids, and lichexanthone. A few species (*Phaeographis haematites*, *P. cinnabarina* (Fée) Mueller Argoviensis, *Phaeographina chrysocarpa* (Raddi) Redinger, among others) have pigments (anthraquinones?).

All specimens were tested with normal thin-layer chromatographic techniques using silica gel aluminum-backed Merck precoated plates. Two solvent systems were always used: hexane-ether-formic acid and benzene-dioxane-acetic acid. Visualization was accomplished with 10% sulfuric acid and heating at 110° C.

A list of the chemicals found and species that contain them is given below. It should be assumed that the chemistry for each species represents that of the type material, unless otherwise indicated, and all other specimens cited.

Lecanoric acid: *Graphis afzelii*

Norstictic acid: *Graphis desquamescens*, *G. dussii*, *G. elegans*, *G. isidiifera*, *G. librata*, *G. lumbricina*, *Phaeographis sub-tigrina*, *Graphina antillarum*, *G. dispersa*, *G. platyleuca* (accessory), *G. pseudoanaloga*, *G. suberythrella*, and *Phaeographina atrovermicularis*

Norstictic acid with stictic and constictic acids: *Graphina collospora*

Protocetraric acid: *Graphina platyleuca*

Psoromic acid: *Graphina columbina*

"Quintaria" unknowns: *Phaeographis exaltata* and *Graphina virginea*

Salazinic acid: *Graphina colliculosa* and *G. marcescens*; *G. platyleuca* (accessory)

Stictic acid: *Graphis dumastioides*, *G. imshaugii*, *G. leptocarpa*, *G. triticea*, *G. turgidula*, *Graphina triphora*, *G. virginea*, and *Phaeographina oscitans*

TLC negative (no phenolic substances present): *Graphis adpressa*, *G. anfractuosa*, *G. anguilliformis*, *G. flexibilis*, *G. glaucescens*, *G. grammitis*, *G. humilis*, *G. insidiosa*, *G. longula*, *G. olivacea*, *G. rigidula*, *G. rimulosa*, *G. subelegans*, *G. subnitidula*, *G. tachygrapha*, *Phaeographis albida*, *P. arthonioides*, *P. haematites*, *P. mordenii*, *P. rosea*, *Graphina acharii*, *G. adscribens*, *G. carneoviridis*, *G. chlorocarpa*, *G. dimidiata*, *G. frumentaria*, *G. illinata*, *G. incrustans*, *G. insculpta*, *G. macella*, *G. nuda*, *G. plurispora*, *G. rufopallida*, *G. vestitoides*, *Phaeographina caesioprui-nosa*, *P. coriaria*, *P. difformis*, *P. elliotii*, and (in part) *P. exaltata*

Pigments: *Phaeographis haematites*

Ecology

The family Graphidaceae is one of the largest groups in the lichens with over 1100 published names. One should not be surprised, therefore, to find that the species have become adapted to a wide

range of habitats and often, as in the case of *Graphis afzelii*, seem to have a wide ecological amplitude in both secondary and primary forests. This is in contrast to the closely related Thelotrema-taceae that are highly restricted to undisturbed rain forest in Dominica (Hale, 1974) and other tropical areas.

We are not able to categorize all the species ecologically even for such a small island as Dominica since many are represented by only one or two collections. However, the areas of mid elevation virgin rain forest generally have the greatest number of species. Of the commoner species the following, for example, appear to be more or less confined to well developed rain forests: *Graphis olivacea* (also rarely found in elfin forest), *Graphina chlorocarpa*, *G. colliculosa*, and *G. illinata*. These species are common in and probably restricted to elfin or mossy forest: *Graphis adpressa*, *G. anguilliformis*, *G. lumbricina*, *G. tachygrapha*, *G. triticea*, *Phaeographis exaltata*, and *P. mordenii*. These occur chiefly in low elevation, disturbed habitats: *Graphis desquamescens*, *Graphina antillarum*, and *G. virginea*. Further notes are given under "Habitat" for each species but these should be considered tentative until more collections are made.

Evolution in the Graphidaceae

In order to speculate on the evolution of non-stromatoid graphids, several assumptions must be accepted. First, one must assume that the group is relatively natural, i.e., monophyletic. Second, since data from genetics and cytology are still lacking, one must assume that at least some phylogeny can be inferred from ontogeny.

Although the pitfalls and fallacies of using ontogeny as a source for evolutionary speculation are well known, there seems little choice in the Graphidaceae. Specifically, stages of spore development may supply the only concrete bases yet available.

The following four observations on spore ontogeny should be considered:

1. All Graphid spores start as a one-loculed (one-celled) structure, progress to two locules, then to four (rarely three) uniseriate chambers, then to multilocular stages.

2. Longitudinal spore septae occur only after most transverse septae have been laid down.

3. Monosporous asci always (?) begin as plurisporous asci, followed by abortion of most spores in their early stages. Monosporous asci occur only (?) in *Graphina* and *Phaeographina*. Four-locular spores always occur as a group of eight per ascus; most spores with only transverse septae also occur as a group of eight per ascus.

4a. Pigmentation of spores occurs last, after spores reach essentially full size and septation.

4b. Pigmentation is accomplished by thickening of walls in all (?) *Phaeographis*, but in very few *Phaeographina* species. Those *Phaeographina* species which do have thickened walls also have rather irregularly distributed spore locules, and the spores are rather small and similar in size to the bulk of *Phaeographis* spores.

From these observations one might draw the following highly speculative conclusions:

1. Species with two- or four-loculed spores are most like primitive (ancestral) stock, unless other data indicate that these forms are reduced or neo-

tenous derivatives.

2. Muriform-spored species are derived from ancestors with *Graphis*-like spores.

3. Monosporous forms are derived from ancestors with plurisporous asci.

4a. Pigmentation may occur at any stage of spore septation, but usually represents the last event in spore development. Therefore sporomorphs which differ only in pigmentation are extremely closely related (i.e., one "step" apart).

4b. As most *Phaeographina* species do not have thick-walled spores, they are probably derived from *Graphina* sporomorphs by added pigmentation, rather than from *Phaeographis* sporomorphs by added septation. The less common thick-walled *Phaeographina* species may be derived from irregularly-loculed *Graphina* ancestors (also rather uncommon) or from *Phaeographis*-like forms.

Putting these speculations together in graphic form, we propose a very hypothetical scheme of evolutionary relationships (Figure 2).

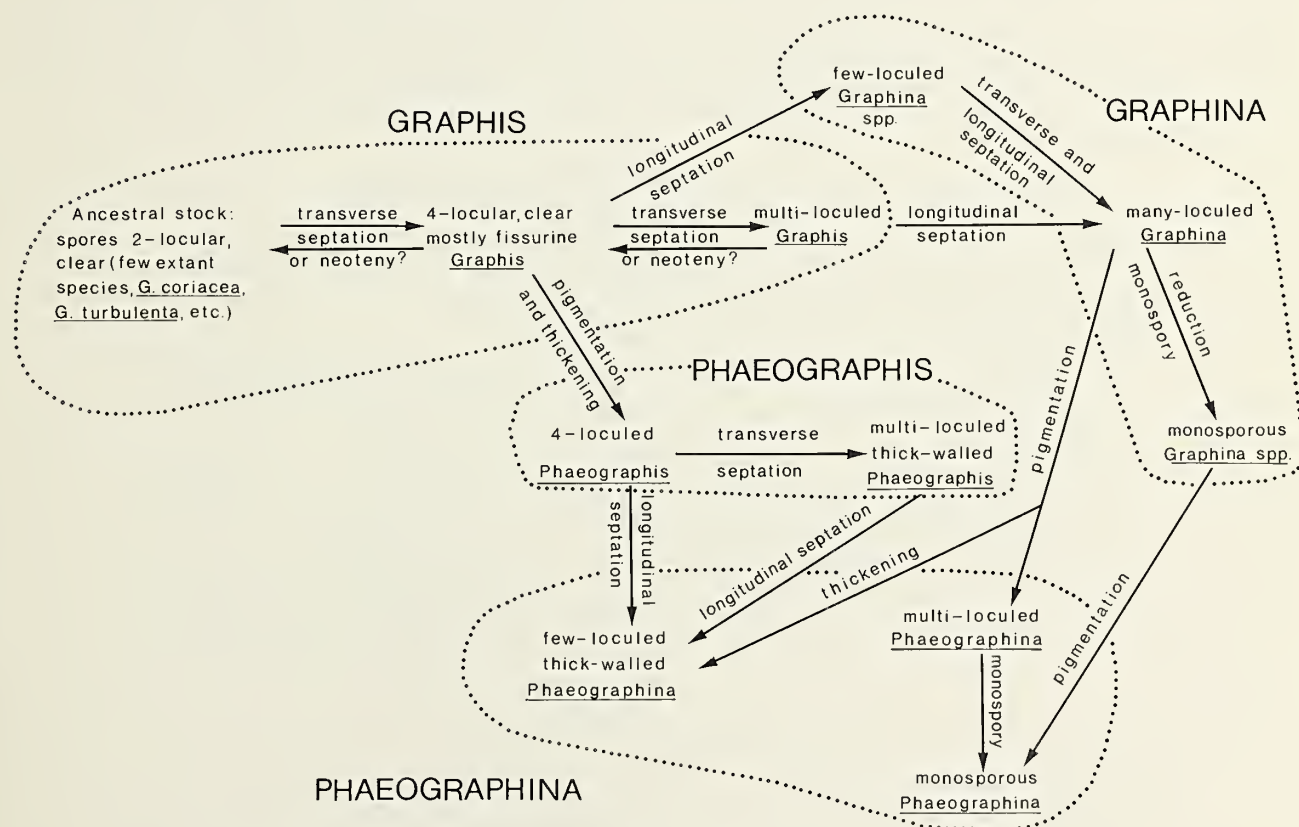


FIGURE 2.—Hypothetical origin and relationships of the genera of the Graphidaceae.

This scheme immediately gives rise to certain questions, problems, and objections, to wit: Where does carbonization fit in this scheme? *Graphis* species with few-loculed spores, supposedly primitive in the proposed arrangement, very rarely show any carbonization. At the same time, lack of carbonization is also the more common condition in the supposedly most advanced groups (i.e., those with monosporous asci and muriform spores). In addition, many of the fissurine *Graphis* species, supposedly primitive, show an apparently specialized (prosoplectenchymatous) upper cortex. One way to resolve these contradictions might be to consider the carbonized *Graphis* species with multilocular spores as equivalent to an ancestral stock, and to regard the fissurine and other forms with very simple spores and little carbonization as derived (reduced) forms, the spore simplicity perhaps arising neotenically.

Another problem arising from this scheme is the admitted artificiality of the present four-genus system for the nonstromatoid taxa. *Phaeographina*, for example, could arise from two fairly disparate stocks.

Most important, perhaps, is to ask what selection pressures may be involved in generating these

spore states? For example: a fissurine *Graphis* would produce a maximum of four germination tubes per spore and hence have a low number of tubes in each of many landing sites. A monosporous muriform species produces a great many tubes in each of fewer sites. Is this relationship significant in terms of colonizing or competing? To the best of our knowledge, there are no data on correlations of spore-types and habitat. The fact that one can find all the spore variants on a single twig does not necessarily mean that there is no competitive advantage associated with the variants. In the *Byrsonima* scrub of western Mexico, for example, all the spore forms occur abundantly, shoulder to shoulder. However, this may be a very equable habitat, comparable to the tropical rain forest for the angiosperms; other more demanding habitats and substrates might reveal significant preferences and correlations. In addition, the abundance of adjacent forms may be misleading in that a succession may be occurring too slowly to be apparent immediately.

The same lack of data exists with respect to distribution of carbonized vs. uncarbonized forms, endo- vs. epiphloeodal thalli, etc. Clearly, much field work remains to be done.

Key to the Genera of Graphidaceae in Dominica

(Although all genera of the Graphidaceae that are known to occur in Dominica are keyed below, the two stromatoid groups, *Glyphis* and *Sarcographa*, are not treated in the text. Each is represented by only one species (Vainio, 1896, 1915.)

1. Ascocarps embedded in prominently raised, stromatoid tissue.
 2. Spores clear, with transverse septae only *Glyphis*
 2. Spores brown, with transverse septae only *Sarcographa*
1. Ascocarps not embedded in raised stromatoid tissue.
 3. Spores clear and hyaline, the walls usually thin.
 4. Spores with transverse septae only *Graphis*
 4. Spores with transverse and longitudinal septae *Graphina*
 3. Spores brown, the walls occasionally thickened.
 5. Spores with transverse and longitudinal septae, the walls rarely thickened *Phaeographis*
 5. Spores with transverse and longitudinal septate, the walls rarely thickened *Phaeographina*

Key to the Species of *Graphis*

1. Spores always four locular.
 2. Ascocarps fissurine, arising as a thalline crack; disc usually concealed or sunken.
 3. Exciple carbonized.
 4. Exciple heavily carbonized laterally, spores 1+ 12. *G. humilis*

4. Exciple carbonized only at labial tips, spores I— (reddish)25. *G. tachygrapha*
3. Exciple totally uncarbonized.
5. Ascocarps usually exposing a red-brown disc in portions, commonly to 10 mm long11. *G. granmitis*
5. Ascocarps fissurine throughout, rarely more than 3 mm long, usually shorter.
6. Ascocarps embedded in swollen tissue ("puffs").
7. Stictic acid present26. *G. triticea*
7. No substances present14. *G. insidiosus*
6. Ascocarps not embedded in swollen tissue.
8. Spores less than 11 μm long; no substances present24. *G. subnitidula*
8. Spores more than 13 μm long; stictic acid present6. *G. dumastioidea*
2. Ascocarps not fissurine; disc broad, obvious, not depressed within a thalline crack.
9. Ascocarps white-powdery; exciple carbonized; lecanoric acid present2. *G. afzelii*
9. Ascocarps not powdery; exciple carbonized; lecanoric acid absent.
10. Thallus isidiate; thalline margin coarsely white-mealy; ascocarps nearly round; norstictic acid present15. *G. isidiifera*
10. Thallus not isidiate; thalline margin not mealy; ascocarps elongate; no substances present11. *G. granmitis*
1. Spores six locular or more.
11. Exciples red-brown to barely carbonized at labial apices10. *G. glaucescens*.
11. Exciples distinctly carbonized.
12. Labia distinctly striate.
13. Exciples with distinct red-yellow areas below the carbonized portions.
14. Thalline margin prominent; spores over 45 μm long20. *G. olivacea*
14. Thalline margin absent or nearly so; spores under 35 μm 23. *G. subelegans*
13. Exciples lacking red-yellow tissue below the carbonized portions (but sometimes dirty-brown below).
15. Ascocarps usually without a prominent thalline margin.
16. Exciples open below; norstictic acid present8. *G. elegans*
16. Exciples closed below; no substances present22. *G. rimulosa*
15. Ascocarps consistently with a thalline margin.
17. Norstictic acid present19. *G. lumbricina*
17. Norstictic acid absent.
18. Exciple open below.
19. Spores usually 70–90 μm long18. *G. longula*
19. Spores usually 50–65 μm long21. *G. rigidula*
18. Exciple closed below.
20. Exciple massively carbonized below9. *G. flexibilis*
20. Exciple barely closed below18. *G. longula*
12. Labia intact or irregular, not distinctly striate.
21. Exciples distinctly open below.
22. Stictic acid only present16. *G. leptocarpa*
22. Norstictic acid only present.
23. Spores less than 36 μm long17. *G. librata*
23. Spores over 45 μm long7. *G. dussii*
21. Exciples distinctly closed below, or the lateral portions of the exciples approaching each other very closely basally.
24. Ascocarps raised, without any thalline margin visible, short (1–2 mm long), *Opegrapha*-like1. *G. adpressa*
24. Ascocarps flush to raised but always with a thalline margin, usually over 2 mm long, not *Opegrapha*-like.
25. Spores under 51 μm long.
26. Stictic or norstictic acid present.
27. Norstictic acid present5. *G. desquamescens*
27. Stictic acid present13. *G. imshaugii*
26. No substances present3. *G. anfractuosa*
25. Spores usually over 60 μm long.
28. Stictic acid present27. *G. turgidula*
28. No substances present4. *G. anguilliformis*

1. *Graphis adpressa*

FIGURE 3a; PLATE 1a

Graphis adpressa Vainio, 1890:119 [type collection: Carassa, Brazil, *Vainio* 1289 (TUR, lectotype)].

DESCRIPTION.—Thallus white, gray, or pale brown, thin but continuous, shining. Ascocarps quite black, raised and protuberant, usually unbranched, no thalline margin visible, 0.5–2 mm long, slender. Disc not visible in surface view. Ascocarp transverse section: hymenium 170–250 μm high, I–; exciple black, closed, lips intact and convergent, frequently with an extremely thin thalline covering. Spores 8/ascus, 10–18 locular, 13–15 \times 50–70 μm , I+ blue.

CHEMISTRY.—No substances present.

HABITAT.—Rain forest above 2600 feet.

DISCUSSION.—*Graphis adpressa* externally resembles an *Opegrapha* or *Melaspilea* and is unlikely to be confused with any other Dominican *Graphis*. It exhibits considerably less variation in morphology than most *Graphids*. Extremely similar but for spore septation and size is *Graphina nuda*.

SPECIMENS EXAMINED.—Fresh Water Lake, 2600–2800 ft, *Hale* 35485, 35487 (US), 2600–2877 ft, *Imshaug* 32849A, 32852A, 32854 (MSC); Trois Pitons, 2900–3150 ft, *Imshaug* 33090 (MSC); Morne Diablotin, 3500–4300 ft, *Imshaug* 32940 (MSC); Micotrin, ca 3000 ft, *Wirth* 464 (US).

2. *Graphis afzelii*

FIGURE 3b; PLATE 1b

Graphis afzelii Acharius, 1814:85 [type collection: Guinea, *Afzelius*, s.n. (H, lectotype; UPS, isotype)].

DESCRIPTION.—Thallus brownish tan to gray, continuous, smooth. Ascocarps usually completely covered by a powdery white thalline layer, appearing black only where this layer is rubbed, usually unbranched, 1.0–6.0 mm long, to nearly 1 mm wide. Disc not visible in surface view. Ascocarp transverse section: hymenium 75–150 μm high, I–; exciple black laterally, brown and closed to pale and open basally, lips convergent, intact, with a prominent thalline covering extending to their apices. Spores 8/ascus, always 4 locular, 6–9 \times 16–23 μm , I+ blue.

CHEMISTRY.—Lecanoric acid (in the thalline apothecial covering only).

HABITAT.—Dry sea-level scrub to virgin upland

rain forest; apparently with broad ecological amplitude.

DISCUSSION.—*Graphis afzelii* is a common pan-tropic species, unique in the family in having lecanoric acid. This acid, along with the distinctive exciple structure, render it unlikely to be confused with any other graphid.

SPECIMENS EXAMINED.—Pointe Round, 100 ft, *Imshaug* 33484A (MSC); Londerry Agricultural Area, 100 ft, *Imshaug* 32897 (MSC); near Madjini, 100 ft, *Hale* 35618 (US); north of Bioche, 200 ft, *Hale* 35644 (US); Can-Dom logging area, Newfoundland, 800 ft, *Hale* 35239, 35446, 35447 (US); 8 miles north of Pont Cassé, 1400 ft, *Wirth* 546 (US); Can-Dom logging area, Dleau Gommier, 1600–1700 ft, *Hale* 35183 (US).

3. *Graphis anfractuosa*

FIGURE 3c; PLATE 1c

Graphis anfractuosa Eschweiler in Martius, 1833:86 [type collection: Caeté, Brazil, s.n. (M, lectotype; G, isotype)].

DESCRIPTION.—Thallus dull white to gray, thin, continuous. Ascocarps partially emergent, the labial tips appearing as slender, flexuose, black, sparingly branched lines 1.0–3.0 mm long. Disc not visible in surface view. Ascocarp transverse section: hymenium (80–) 90–130 μm high, I–; exciple black laterally, frequently dark brown to black below, usually closed, lips more or less intact, convergent. Spores 8/ascus, 8–12 locular, 9–10 \times 40–50 μm , I+ blue.

CHEMISTRY.—No substances present.

HABITAT.—Rain forest lower branches, ca. 1400 feet (good specimen); coastal scrub (poor specimen).

DISCUSSION.—The lectotype specimen of *Graphis anfractuosa* is large but apparently without spores; the isotype at Geneva is quite small but fertile.

Very similar is *Graphis desquamescens*, which differs in having smaller spores and norstictic acid.

SPECIMENS EXAMINED.—Scotts Head, sea level, *Wirth* 538 (US); Emerald Pool, ca 1400 ft, *Wirth* 504a (US).

4. *Graphis anguilliformis*

FIGURE 3d; PLATE 1d

Graphis anguilliformis Taylor, 1847:152 [type collection: St. Vincent, s.n. (FH, lectotype)].

DESCRIPTION.—Thallus tan to light brown, thick, glossy, frequently cracked. Ascocarps large, protuberant, unbranched to sparingly branched, straight

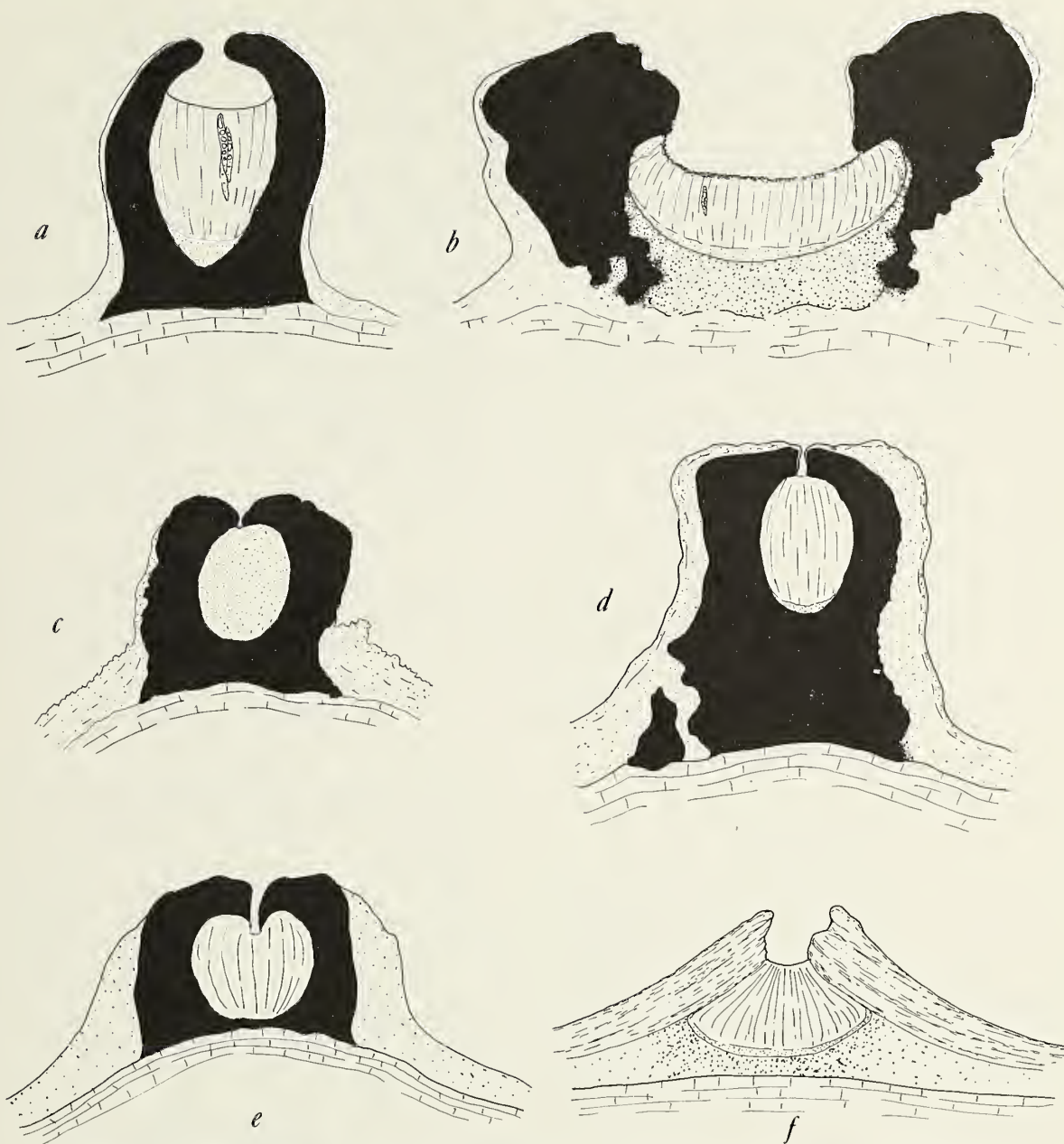


FIGURE 3.—Cross sections of apothecia of *Graphis*: a, *G. adpressa* (Vainio 1289); b, *G. afzelii* (lectotype in H); c, *G. anfractuosa* (lectotype in G); d, *G. anguilliformis* (lectotype in FH); e, *G. desquamescens* (Glaziou 5082); f, *G. dumastioides* (Fink 723 in MICH).

to flexuose in the larger lirellae, covered at least half by a concolorous thalline margin, the exposed labial tips black, 0.5–10 mm long, to nearly 0.5 mm wide. Disc not visible in surface view. Ascocarp transverse section: hymenium 190–250 μm high (to 375 μm in a few extreme cases), I–; exciple black, massive, closed, lips entire, convergent, thalline

margin prominent. Spores (2–) 4–6 (–8?)/ascus, 12–18 locular, 12–15 \times (65–) 75–110 (–130) μm , I+ blue.

CHEMISTRY.—No substances present.

HABITAT.—Rain forest above 1500 feet, up into elfin forest.

DISCUSSION.—*Graphis anguilliformis* ("anguillae-

formis" in the original description) is the commonest graphid in Dominica; we have also seen abundant material of this very large species from Puerto Rico, Mexico, and Colombia. A number of species are quite similar, as follows.

Opegrapha rhizocola Fée (1824) is probably an earlier name for *G. anguilliformis* but the type (G) is sterile and very small. In light of the depauperate type and the common usage of Taylor's name, we suggest that the Fée name should be permanently dropped.

Graphis cooperta Zenker (1829) is supposedly a synonym of *O. rhizocola* (fide Mueller Argoviensis, 1887), but we have not been able to locate the type.

Graphis seminuda Mueller Argoviensis (1891) is likely to prove a synonym of *G. anguilliformis*; an isotype specimen (US) differs only in the more or less open exciple.

Graphis tumidula (Fée) Sprengel (1827) is quite close; it differs in size (hymenium frequently 400 μm high) and in the very large spores (40 locular, to 300 μm long). According to Mueller Argoviensis (1887) this species is a synonym of *Graphis cinerea* Fée (1824); however, the type of *G. cinerea* (G) is striate.

Graphis turgidula Mueller Argoviensis differs in having stictic acid.

Graphis flexibilis differs only in being somewhat smaller, and in having striate labia.

SPECIMENS EXAMINED.—Can-Dom logging area, Dleau Gommier, 1600–1700 ft, *Hale* 35154 (US); Can-Dom logging area, Pont Cassé, 2000 ft, *Hale* 35084, 35112 (US); Can-Dom logging area, Brantridge Estate, 1700 ft, *Hale* 35282 (US); Morne Anglais, 300–3600 ft, *Hale* 35326a, 35349, 35351 (US), *Elliott* s.n. (TUR); Boiling Lake, 2400–3000 ft, *Hale* 35759, 35760 (US); Fresh Water Lake, 2600–2877 ft, *Imshaug* 32848 (MSC); Boeri Lake, 2750 ft, *Imshaug* 33225 (MSC); Central Forest Reserve, 1500 ft, *Imshaug* 33554A (MSC); Morne Diablotin, 3000–3500 ft, *Imshaug* 32955 (MSC); 2200–2600 ft, *Hale* 38174, 38191 (US).

5. *Graphis desquamescens*

FIGURE 3e; PLATE 1e

Graphis desquamescens (Fée) Zahlbruckner, 1909:108.

Opegrapha desquamescens Fée, 1874:24 [type collection: Brazil, Glaziou 5082 (M, lectotype)].

DESCRIPTION.—Thallus white to off-white, continuous, slightly roughened and matte. Ascocarps flush to emergent, slender, flexuose, black, fre-

quently branched, usually with a low thalline margin, (1–) 2–4 (–6) mm long. Disc barely visible in surface view. Ascocarp transverse section: hymenium 60–70 (–120) μm high, I–; exciple black, more or less closed, labia convergent, usually entire but barely striate in occasional sections. Spores 8/ascus, 6–9 locular, 6–8 \times (20–) 23–35 (–50) μm , I+, blue.

CHEMISTRY.—Norstictic acid (crystal test only for the lectotype).

HABITAT.—Dry scrub from sea level to 700 feet.

DISCUSSION.—This species occurs throughout the Neotropics; it has been reported (probably correctly) from Japan by Nakanishi (1966). Very similar to *Graphis desquamescens* is *G. intricata* Fée (1824), separable only by the smaller spores (less than 15 μm long) in the latter. Also similar is *G. anfractuosa*, which lacks norstictic acid and has somewhat larger spores.

SPECIMENS EXAMINED.—Rodney's Rock, sea level, *Hale* 35581 (US); north of Mero, 50 ft, *Hale* 35067, 35449, 35727 (US); Grande Savanee, 200–250 ft, *Imshaug* 33285A, 33291A (MSC); Mt. St. Mary's, 600–700 ft, *Imshaug* 33448A (MSC).

6. *Graphis dumastioides*

FIGURE 3f; PLATE 1f

Graphis dumastioides Fink, 1927:213 [type collection: Mameyes, Puerto Rico, *Fink* 723 (MICH, lectotype; FH, US, isotypes)].

DESCRIPTION.—Thallus brown to greenish tan, glossy, continuous, rather thick for a fissurine species (to 150 μm), with a distinct prosoplectenchymatous upper layer. Ascocarps appear as flexuose, unbranched to sparingly branched fissures in the thallus, the margins usually not concolorous with the rest of the thallus, 0.5–4.0 mm long. Disc sunken and usually not easily visible in surface view. Ascocarp transverse section: hymenium 60–100 μm high, I–; exciple rudimentary at best, the lips consisting of barely modified uncarbonized thalline tissue with included bark cells. Spores 8/ascus, always 4 locular, (6–) 8–9 \times (14–) 18–25 μm , I– or I+ slow, faint and reddish.

CHEMISTRY.—Stictic acid.

HABITAT.—Rain forest.

DISCUSSION.—For a discussion of the fissurine complex of species, see *Graphis triticea*.

SPECIMEN EXAMINED.—Road to Morne Jean, 2000–2400 ft, *Hale* 37722 (US).

7. *Graphis cf. dussii*

FIGURE 4a; PLATE 2a

Graphis dussii Vainio, 1899:255 [type collection: Guadeloupe, *Duss* 515 (TUR, lectotype)]

Phaeographis dussii (Vainio) Zahlbruckner, 1923:371.

DESCRIPTION.—Thallus off-white, thick, glossy. Ascocarps in type oryzaeform only, mostly 0.5×1.0 mm, in Dominican specimen to 3.0 mm long, both usually unbranched and more or less straight, with a low thalline margin. Disc usually not visible in surface view. Ascocarp transverse section: hymenium 140–150 μm high, I–; exciple black laterally, open below, lips convergent, entirely to barely crenate. Spores 6–8/ascus, (10–) 12–16 locular, $6\text{--}10 \times 60\text{--}100$ μm (46 μm long fide Vainio, but none so short found on the type), I+ blue.

CHEMISTRY.—Norstictic acid.

HABITAT.—Upland rain forest.

DISCUSSION.—Although Vainio described the spores of *Graphis dussii* as darkened, we can find only typical *Graphis* spores in the type.

On the type specimen, only short oryzaeform lirellae are present; the Dominican material has mostly longer ascocarps, with very few as short as in the type. As apothecial length is rather variable in the family, we are assuming that additional collections will bridge the gap between these two specimens. We are thus using the name to cover the largest specimens, with large spores and norstictic acid, of the *Eugraphis* alliance. For a more complete discussion of this complex group, see under *Graphis leptocarpa*.

SPECIMEN EXAMINED.—Morne Diablotin, 3200–4600 ft, *Hale* 35443 (US).

8. *Graphis elegans*

FIGURE 4b; PLATE 2b

Graphis elegans (Smith) Acharius, 1814:85.

Opegrapha elegans Smith in Smith and Sowerby, 1807:16 [type collection: Britain (BM); only a cross-section of the BM specimen seen].

DESCRIPTION.—Thallus grayish white, continuous, glossy to slightly roughened. Ascocarps black, raised, flexuous, usually unbranched, thalline margin usually absent, striae distinctly visible from above, 2.0–6.0 mm long, less than 0.5 mm wide. Disc not visible in surface view. Ascocarp transverse section:

hymenium 90–100 μm high, I–; exciple black, more or less open below, lips convergent, from barely to very striate (on same specimen). Spores 8/ascus, 9–12 locular, $10\text{--}11 \times 50\text{--}60$ μm , I+ blue.

CHEMISTRY.—Norstictic acid (see discussion).

HABITAT.—Secondary and mossy forests above 1800 feet.

DISCUSSION.—Without having seen the type of *Graphis elegans*, the identification of the Dominican material is somewhat uncertain, but our material matches the “classic” concept of the European species very closely. In addition, at least some of the specimens from northern Europe also contain norstictic acid. Specimens are also recorded from New Zealand (Hayward, 1978) that match both the Dominican and European material very closely. If these identifications are all correct, then *G. elegans* must be a cosmopolitan species.

Closely related to *G. elegans* are the species of the *G. rimulosa* complex, from which the former is distinguished by larger spores and the presence of norstictic acid.

SPECIMENS EXAMINED.—Giraudel, 1800–2000 ft, *Hale* 35476 (US); Fresh Water Lake, 2600–2800 ft, *Hale* 35325 (US).

9. *Graphis flexibilis*

FIGURE 4c; PLATE 2c

Graphis flexibilis Krempelhuber, 1876:414 [type collection: Brazil, *Glaziou* 5106 (M, lectotype)].

DESCRIPTION.—Thallus gray to white, usually smooth and glossy, occasionally somewhat roughened and cracked, thick, cortex prosoplectenchymatous or nearly so. Ascocarps prominently raised, mostly flexuose, occasionally branched, black and obviously striate above, half to nearly completely covered by a thalline margin, 2.0–4.0 mm long (commonly longer in non-Dominican material), slender. Disc not visible in surface view. Ascocarp transverse sections: hymenium (50–) 100–150 μm high, I–; proportionately small for the massively carbonized exciple (ca. 300 μm high), exciple always quite closed below, lips convergent, with 1–4 striae. Spores 6–8/ascus, (15–) 20–30 locular, $13\text{--}16 \times 60\text{--}150$ (–190) μm (60–110 μm in the type specimen), I+ blue.

CHEMISTRY.—Type, P–, no TLC made; Dominican material, no substances present.

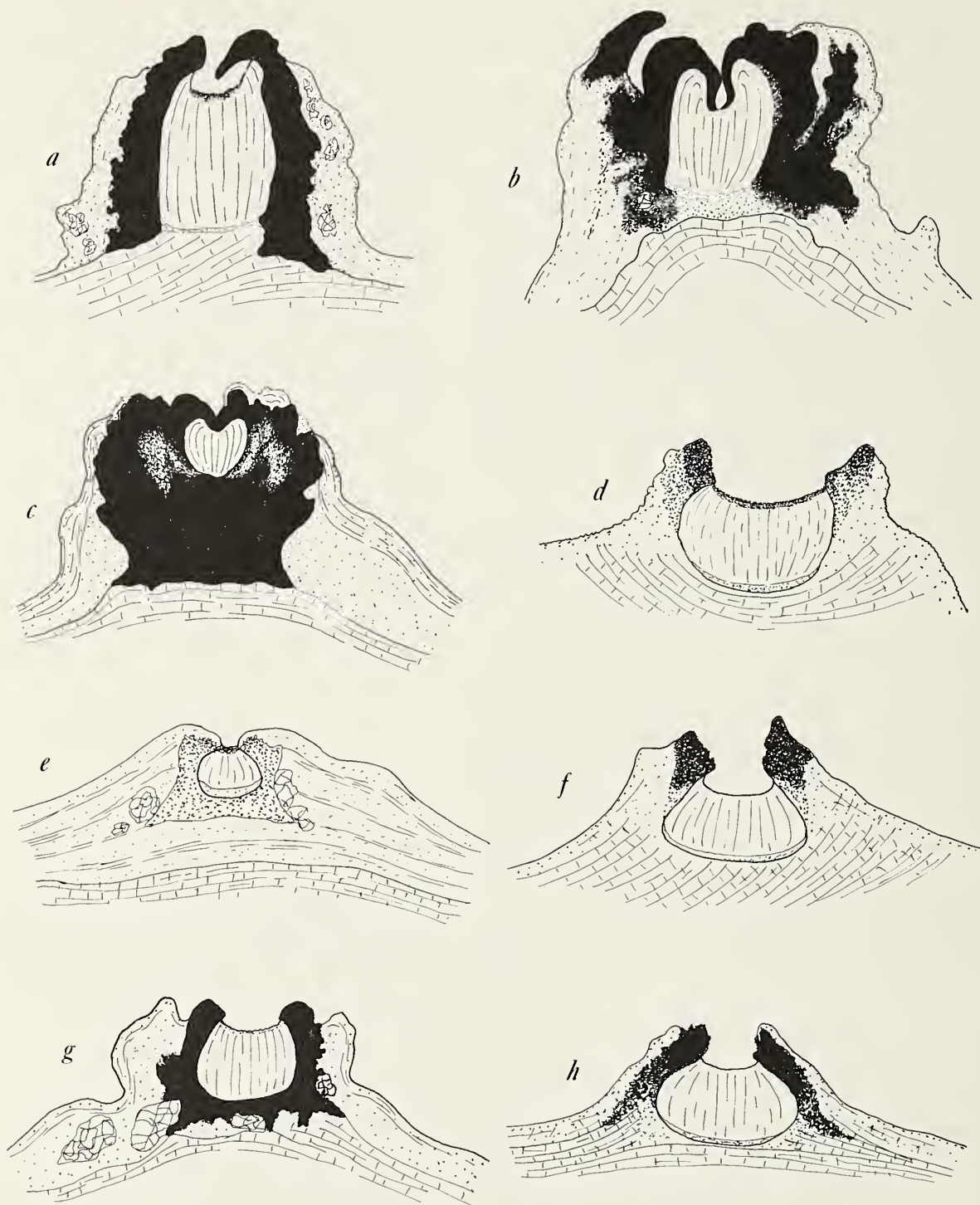


FIGURE 4.—Cross sections of apothecia of *Graphis*: a, *G. dussii* (Duss 515); b, *G. elegans* (lectotype in BM); c, *G. flexibilis* (Glaziou 5016); d, *G. glaucescens* (lectotype in G); f, *G. imshaugii* (Imshaug 32724B); g, *G. humilis* (Merrill 9067); h, *G. humilis* (Hale 35698).

HABITAT.—Below the lower edges of the wet rain forest.

DISCUSSION.—Externally *Graphis flexibilis* strongly resembles *G. anguilliformis* and *Graphina acharii* and can be considered a sporomorph of the latter. Many other species must be treated in any discussion of *G. flexibilis*, as follows.

Graphis angustata Eschweiler (1833) is supposedly an earlier name for *G. flexibilis* (fide Zahlbruckner, 1923); however, the type (M!) has apparently always been found to be sterile (see Mueller Argoviensis 1888b:509). We could find no spores on the type, and hence this name should be discarded permanently. *Graphis angustata* var. *denudatum* Vainio (1915) has a proportionally small hymenium, nearly intact lips, contains an unknown substance, and is hence quite dissimilar to the "classic" concept of *G. angustata*; *G. angustata* var. *ingarum* Vainio (1915), also unrelated, belongs in the *Eugraphis* alliance.

Graphis cinerea Fée (1824) is very similar in morphology and anatomy; although the type now seems to be sterile, Mueller Argoviensis (1887) found very large spores (to 250 μm), with only 1–3 per ascus. For the moment, this species can thus be separated from *G. flexibilis* by its spores.

Graphis calcea (Fée) Massalongo (1853) can tentatively be separated by its lower ascocarps (nearly flush) and fewer striae.

Graphis congesta (Fée) Mueller Argoviensis (1887) is much like *G. lumbricina* (below), but differs in its shorter, asteroidly-branched ascocarps.

Graphis longula differs in being more sunken, smaller, and in having a nearly open exciple.

Graphis lumbricina differs in the presence of norstictic acid and in the occasionally open exciple.

Graphis olivacea is separable only by the paler red-yellow excipular base.

Graphis rigidula can tentatively be separated by its open exciple and smaller size.

Graphis tumidulella Fink (1927) is separable only by its smaller spores (under 50 μm).

SPECIMENS EXAMINED.—Bois Serpe, ca. 1000 ft, *Imshaug* 3272A (MSC); Ridgefield Estate, 1100–1200 ft, *Imshaug* 33360 (MSC); Shawford Estate, *Elliott* 1854 p.p. (TUR).

10. *Graphis glaucescens*

FIGURE 4d; PLATE 2d

Graphis glaucescens Fée 1824:36 [type collection: South

America, s.n. (G, lectotype)].

DESCRIPTION.—Thallus white, continuous, minutely roughened. Ascocarps concolorous with the thallus, more or less black only where the thalline covering is rubbed, slightly raised, branched and flexuose, 1.0–3.0 mm long, slender. Disc occasionally visible as a slightly darker central area. Ascocarp transverse section: hymenium 75–100 μm high, I–, epihymenium somewhat darkened; exciple more or less open, lips more or less convergent, apically red-brown to barely carbonized, paler below. Spores 4–) 6 (–8)/ascus, 6–12 locular, 7–12 \times (35–) 42–55 μm , I+ blue.

CHEMISTRY.—No substances present.

HABITAT.—Lowland cultivated areas.

DISCUSSION.—*Graphis caesioglauca* Redinger (1935) is indistinguishable, externally and internally, from *G. glaucescens*. Transverse sections of the type (*Malme* 1526, S) indicate the same labial structure, and the Redinger illustrations are incorrect. We have not yet determined the chemistry of *G. caesioglauca*.

SPECIMENS EXAMINED.—Brookhill Estate, 100–150 ft, *Imshaug* 33313A (MSC).

11. *Graphis grammitis*

PLATE 2e

Graphis grammitis Fée 1824:47 [type collection: South America, s.n. (G, lectotype)].

DESCRIPTION.—Thallus thick, prosoplectenchymatous, continuous, gray to greenish brown, usually glossy. Apothecia nearly fissurine at first, then strongly gaping, but with margins not separating laterally from the disc or hymenium as in "typical" fissurine species, occasionally branched, flexuose, commonly 10 mm long, slender. Disc exposed in at least a portion of the ascocarps, red-brown. Ascocarp transverse section: hymenium 60 μm high (35–40 in the type), epihymenium usually darkened, I–; exciple barely closed, yellow-brown to red-brown, lips convergent to strongly spreading, apically sometimes darkened. Spores 8/ascus, always 4 locular, 4–8 \times 10–14 μm , I+ blue.

CHEMISTRY.—No substances present.

HABITAT.—Elfin forest and upland rain forest (Dominica only).

DISCUSSION.—In early stages, the ascocarps of *Graphis grammitis* are quite fissurine, and appear

to be a nongaping equivalent of *G. dumastii*. (The type, which is quite poor, consists mostly of this fissurine condition). Later stages, however, develop rather prominent margins and appear very much like *Graphina colliculosa* externally.

Quite similar in morphology and anatomy is *Graphis floridana* Tuckerman (1888); the latter species, however, has norstictic acid and probably has submuriform spores (and hence is referable to *Graphina*).

SPECIMENS EXAMINED.—Layou Road, northwest of Pont Cassé, 1400 ft, *Hale* 38005 (US); Elfin woodland, Boeri Lake, 2750 ft, *Imshaug* 33208 (MSC).

12. *Graphis humilis*

FIGURE 4h; PLATE 2f

Graphis humilis Vainio, 1921:256 [type collection: Philippines, Merrill 9067 (TUR, not seen; US, isotype)].

DESCRIPTION.—Thallus dirty white to pale tan, thin (endophloeodal?), continuous, matte. Ascocarps fissurine, barely raised, mostly straight and unbranched, the dark exciples showing through a thin thalline covering, 0.5–2.0 mm long. Disc not visible in a surface view. Ascocarp transverse section: hymenium 60–75 μm high, I–; exciple quite open (rudimentary) basally, lips convergent, carbonized apically only (type specimen) to apically and laterally. Spores 8/ascus, always 4 locular, 7–9 \times 14–25 μm , I+ blue.

CHEMISTRY.—No substances present.

HABITAT.—Wet lowland and coastal forest.

DISCUSSION.—The Dominican material matches the Philippine isotype closely, differing only in having somewhat larger spores and more carbonized labia. The carbonization makes this species distinct in the fissurine alliance; the closest relative is probably *Graphis tachygrapha*, which has less carbonization, and I– spores. A more complete discussion of the complex alliance of fissurine *Graphis* species may be found under *G. triticea*.

A sporomorph of *G. humilis* (with I– spores, however) is *Phaeographis arthonioides*.

SPECIMEN EXAMINED.—Madjini, 100 ft, *Hale* 35698 (US).

13. *Graphis imshaugii*, new species

FIGURE 4f; PLATE 3a

DESCRIPTION.—Thallus continuus, laevis, proso-

plectenchymatus. Apothecia subimmersa vel semi-emergentia, flexuosa, ramulosa, 2–4 mm longa, margine thallino crassiusculo, cum thallo concolore, ab eo fissura tenuissima separato. Excipulum vulgo integrum vel subintegrum, fuligineum, labiis integris, erectis; hymenium 120–140 μm altum, I–. Asci 8 spori; sporae decolores, 8–10 loculares, 6–9 \times (17–) 23–35 μm , I+ coeruleae.

Thallus continuous, thick, glossy, green-gray, cortex prosoplectenchymatus. Ascocarps usually raised (in type) to nearly flush (in the Mexican specimen), flexuose, commonly branched, 2–4 mm long, slender, the prominent thalline margin commonly separating from the exciple, which is black and pruinose. Disc barely visible in surface view. Ascocarp transverse section: hymenium 120–140 μm high, I–; exciple black, closed to nearly open, lips intact to rarely slightly striate, upright to somewhat spreading. Spores 8/ascus, 8–10 locular, 6–8 \times (17–) 25–35 μm , I+ blue.

CHEMISTRY.—Stictic acid, constictic acid.

HOLOTYPE.—Cultivated area, South Chiltern Estate Road, 1500–1700 feet, *Imshaug* 32724B (MSC).

DISCUSSION.—*Graphis imshaugii* is closely related to *G. subamylacea* Zahlbruckner (1921), from Mexico. The former species differs in the glossy (not farinulose) thallus, more robust ascocarps, and in the distinct fissure which separates the exciple and the thalline margin.

Pringle 412 (Tamaulipas, Tampico, Mexico, MICH), previously identified by us (Wirth and Hale, 1963) as *G. subamylacea*, is properly referable to *G. imshaugii*.

14. *Graphis insidiosa*

FIGURE 5a; PLATE 3b

Graphis insidiosa (Knight and Mitten) Hooker fil., 1867:586. *Fissurina insidiosa* Knight and Mitten, 1860:102 [type collection: New Zealand, *Knight* 259 (BM, lectotype designated by Hayward, 1978)].

Graphis beaumontii Tuckerman, 1888:124 [type collection: Alabama, USA, *Beaumont* 324 (FH, lectotype)].

Graphis interversa Nylander, 1889:49 [type collection: Florida, USA, *Eckfeldt* 339 (H, lectotype)].

Graphis lactea var. *clausa* Vainio, 1915:163 [type collection: Soufrière, Dominica, *Elliott* 1511 (TUR, lectotype)].

DESCRIPTION.—Thallus greenish to green-tan, usually thick and cracked, glossy but with frequent

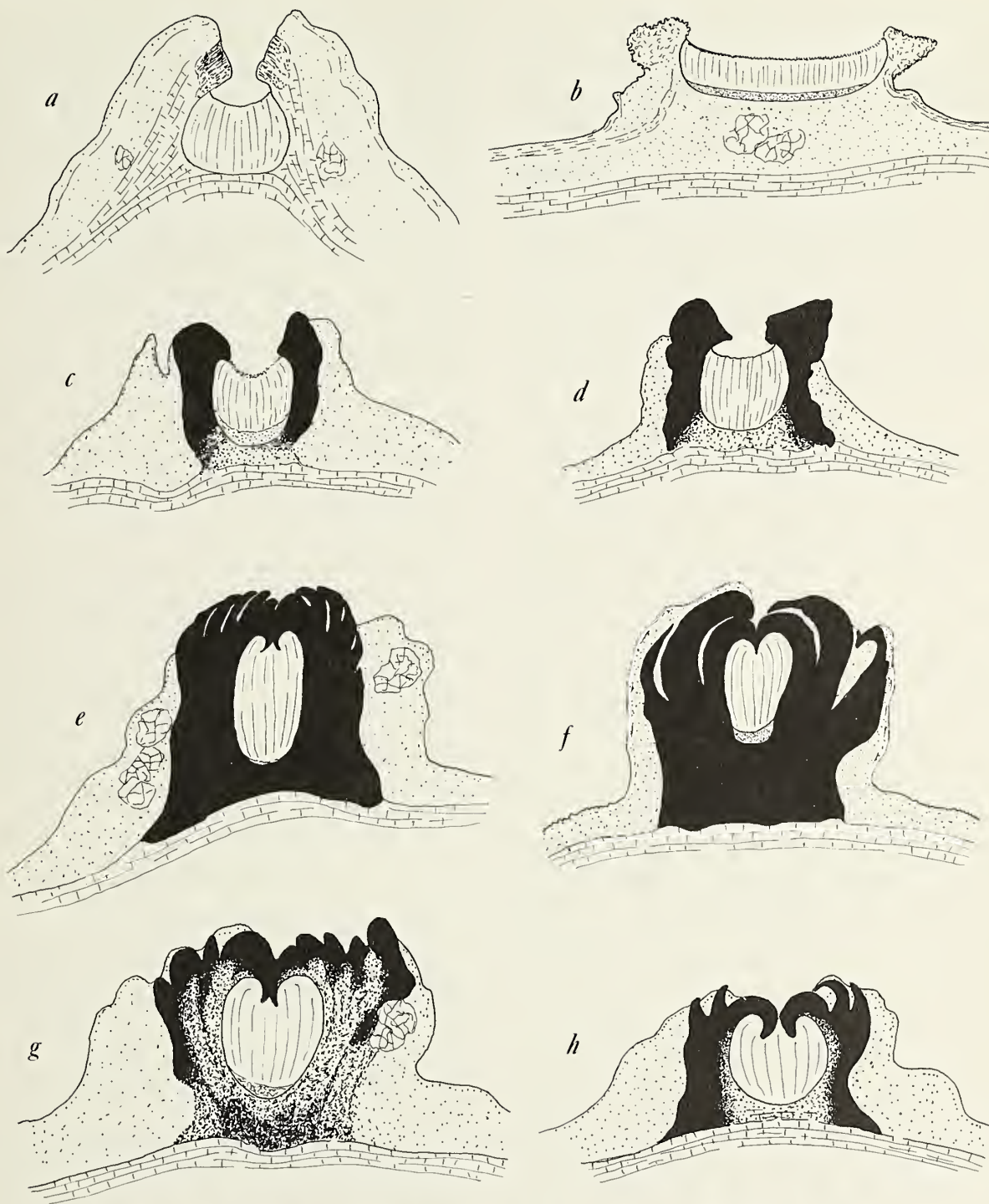


FIGURE 5.—Cross sections of apothecia of *Graphis*: a, *G. insidiosa* (Knight 259); b, *G. isidiifera* (Hale 35179); c, *G. leptocarpa* (lectotype in G); d, *G. librata* (Knight s.n.); e, *G. longula* (Glaziou 5497); f, *G. lumbricina* (Duss 1036); g, *G. olivacea* (Malme 2267); h, *G. rigidula* (Pit-tiers s.n.).

bumps and rugosities, in section showing a poorly developed prosoplectenchymatous cortex. Ascocarps starting as fissurine cracks, usually developing raised and swollen concolorous thalline margins, usually unbranched, 1–4 mm long. Disc usually not visible in surface view. Ascocarp transverse section: hymenium 90–140 μm high, I–; exciple pale, open, lips convergent to slightly gaping, pale to barely darkened apically, rudimentary below. Spores 8/ascus, always 4 locular, (5–) 8–11 \times (11–) 13–22 (–24) μm , I– or I+ slow, reddish.

CHEMISTRY.—No substances present in all except *Hale* 35313, which has 2–3 unknown spots in TLC.

HABITAT.—Wet lowland forest (US), wet upland forest (Dominica).

DISCUSSION.—Examination of the types of *Graphis insidiosa*, *G. beaumontii* and *G. interversa* indicates that these three taxa are identical. The type of *G. lactea* var. *clausa* differs in lacking the cracking of the thallus and in having rather shorter, smaller ascocarps. The nearly continuous, uncracked thallus is also found in the *Hale* and *Wirth* collections; we feel, however, that these differences are too minor to warrant naming.

Graphis insidiosa is most similar to *G. triticea*, from which it differs in lacking stictic acid, having lower ascocarps with a less elaborate exciple, and in a less prominently prosoplectenchymatous cortex. The two species are, however, quite similar and are most easily separated by their chemistry.

A more complete discussion of the fissurine complex may be found under *Graphis triticea*.

SPECIMENS EXAMINED.—Can-Dom logging area, Dleau Gommier, 1600–1700 ft, *Hale* 35313 (US); Micotrin, ca 3000 ft, *Wirth* 463A (US).

15. *Graphis isidiifera*, new species

FIGURE 5b; PLATE 3c

DESCRIPTION.—Thallus laevis, isidiatus; stratum corticale prosoplectenchymatum. Apothecia immersa, rotunda vel sublirellina, ca. 1 mm longa, 0.5 mm lata, margine thallino, crasso, pallido, farinuloso, discum bene superante, disco dilatato, salmonneo. Excipulum integrum, pallidum, labiis integris, divergentibus; hymenium 70–80 μm altum, I–. Asci 8 spori; sporae decolores, 4 loculares, 4–6 \times 12–13 μm , I–.

Thallus thick, cracked, glossy, pale greenish gray, distinctly isidiate, cortex prosoplectenchyma-

tous. Ascocarps with prominent white mealy margins, nearly round to quite irregular, clumped and branched, ca. 1 mm long, 0.5 mm wide. Disc quite exposed, pale salmon-pink, lightly pruinose, Ascocarp transverse section: hymenium 70–80 μm high, I–; exciple closed, pale, lips entire, spreading. Spores 8/ascus, always 4-locular, 4–6 \times 12–13 μm , I–.

CHEMISTRY.—Norstictic acid, unknown substance.

HOLOTYPE.—Virgin upland rain forest, Can-Dom logging area at Dleau Gommier, 1600–1700 feet, *Hale* 35179 (US).

DISCUSSION.—*Graphis isidiifera* is unlikely to be confused with any other *Graphis* species. The combination of isidia, cracked prosoplectenchymatous thallus, white-margined irregular ascocarps and flesh colored disc render this species quite distinct. It is probably related to the fissurine *Graphis* species, but differs from them in the very broad disc and prominent mealy margin.

Isidia are very rare in the Graphidaceae; to the best of our knowledge, the only other tuberculate-isidiate species occur in *Graphina*, (viz., *Graphina dimorphodes* (Nylander) Zahlbruckner, 1923), *Graphina dealbata* (Nylander) Mueller Argoviensis (1895a), and its close allies *G. albostrata* (Vainio) Zahlbruckner (1923), *G. heteroplacoides* Redinger (1933), *G. rimulosa* Redinger (1933), and *Phaeographina* (= *Graphina*!) *includens* (Vainio) Zahlbruckner (1923).

16. *Graphis leptocarpa*

FIGURE 5c; PLATE 3d

Graphis leptocarpa Fée, 1824:36 [type collection: South America, *Humboldt and Bonpland* s.n. (*G.* lectotype)].

DESCRIPTION.—Thallus white to off-white, continuous, smooth to slightly roughened. Ascocarps raised, black, unbranched to occasionally branched, straight to somewhat flexuose, with a slightly raised thalline margin, 1–3 mm long, slender. Disc not visible in surface view. Ascocarp transverse section: hymenium 90–100 μm high, I–; exciple black laterally, absent below, lips more or less convergent. Spores 8/ascus, 8–9 locular, 5–8 \times 16–23 μm (in the type) to 42 μm (in the Dominican and other material), I+ blue.

CHEMISTRY.—Stictic acid (and usually constictic acid).

HABITAT.—From sea level scrub to rain forest. Probably pantropical.

DISCUSSION.—The *Eugraphis* alliance is one of the most frustrating species complexes in the family. The type species of the Graphidaceae, *Graphis scripta*, belongs here; unfortunately this species has not yet been typified properly. In addition, as *G. scripta* is probably a north temperate population, we have refrained from calling any tropical material by this name.

Of the numerous names published before 1900, the following must be considered in any discussion of tropical eugraphids (i.e., those with dimidiate carbonized exciples and spores in the 20–40 μm range):

Graphis lineola Acharius (1810) is probably the oldest and best name for those tropical eugraphids which are P– (and presumably TLC negative, although as far as we know the type has not yet been chromatographed).

Graphis tenella Acharius (1814), another P negative species, may not belong in this complex at all, even though the “classic” concept of the species places it here. Type material of *G. tenella* at Helsinki has striate labia; if all typical material is striate, then the historical concept of the species is incorrect.

Graphis furcata Fée (1824), which is TLC negative, is probably synonymous with *G. lineola*.

Graphis pavoniana Fée (1824), another TLC negative type, may be distinct from *G. lineola* in being larger overall, with only 4–6 larger spores (to 50 μm) per ascus.

Graphis librata is the norstictic equivalent of *G. lineola* (P–) and *G. leptocarpa* (stictic acid).

Graphis caesiella Vainio (1890), with norstictic acid, differs from *G. librata* primarily in having pruinose ascocarps and discs.

Graphis dussii (above), with norstictic acid, differs from *G. librata* in overall size and in having larger spores.

SPECIMENS EXAMINED.—Pointe Michel, 200 ft, *Imshaug* 33109A (MSC); Morne Conliabon, *Elliott* 1535 (TUR).

17. *Graphis librata*

FIGURE 5d; PLATE 3e

Graphis librata Knight, 1884:404 [type collection: New Zealand, *Knight* 67:23 (WELT, lectotype designated by Hayward, 1978)].

Graphis crebra Vainio, 1899:256 [type collection: Guadeloupe, *Duss* 541 (TUR, lectotype)].

Graphis plumierae Vainio, 1915:161 [type collection: Guadeloupe, *Duss* 1189 (TUR, lectotype)].

Graphis tenellula Vainio 1915:169 [type collection: Santo Domingo, *Raunkiaer* 490 p.p. (TUR, lectotype)].

DESCRIPTION.—Thallus gray-white, continuous to matte. Ascocarps quite variable even on a single thallus, usually more or less raised, straight to flexuose, commonly branched, black, the thalline margin prominent but low, 1–4 mm long, slender. Disc not visible in surface view. Ascocarp transverse section: hymenium 50–100 μm high, I–; exciple quite open below, lips carbonized, entire, more or less convergent; spores 8/ascus, 6–8 locular, 5–9 \times 18–35 μm , I+ blue.

CHEMISTRY.—Norstictic acid.

HABITAT.—Coastal scrub to lower rain forest.

DISCUSSION.—*Graphis librata* is the norstictic equivalent of *Graphis leptocarpa*; for a more complete discussion of the tropical *Eugraphis* complex, see the latter species.

SPECIMENS EXAMINED.—Roseau Botanic Garden, ca 100 ft, *Wirth* 468 (US); Pointe Michel, 200 ft, *Imshaug* 33112A (MSC); Coulibistri, 200 ft, *Hale* 35757 (US); Emerald Pool, *Wirth* 504B (US).

18. *Graphis longula*

FIGURE 5e; PLATE 3f

Graphis longula Krempelhuber, 1876:414 [type collection: Brazil, *Glaziov* 5497 (M, lectotype)].

Graphis flavicans Mueller Argoviensis, 1895a:457 [type collection: Rio, Brazil, *Glaziov* 5498 p.p. (M, lectotype)].

Phaeographis longula (Krempelhuber) Zahlbruckner, 1923: 379.

DESCRIPTION.—Thallus white, greenish white, or gray, continuous, smooth and glossy to slightly roughened and bumpy. Ascocarps more or less emergent, black apically, half to two-thirds covered by the prominent thalline margin, usually straight and unbranched, obviously striate, 1–6 (–10) mm long, slender. Disc not visible in surface view. Ascocarp transverse section: hymenium 60–90 μm high, I–; exciple black, more or less closed to barely open (variable even within a single thallus), lips convergent, striate (appearing only crenate when the grooves are abundant and closely packed). Spores (?4–) 6–8/ascus, (8–) 10–17 locular, 9–13 \times (40–) 70–90 μm , I+ blue.

CHEMISTRY.—Type of *Graphis longula* P., no TLC available; type of *G. flavicans* and Dominican specimens, no substances present.

HABITAT.—Lower edges of rain forest.

DISCUSSION.—The types of *Graphis longula* and *G. flavicans* are extremely similar; note the consecutive collector's numbers.

The exciple cross-section illustrated for the type of *G. longula* in Wirth and Hale (1963) is misleading; thinner sections reveal that the barely crenate appearance is, in fact, a result of a very closely packed deep striae (an excellent example of the pitfalls awaiting the graphidologist).

We have seen material referable to *G. longula* from Mexico and Costa Rica, indicating that it will probably be found through most of the Neotropics.

Very similar (and perhaps synonymous) is *Graphis rigidula* (p. 21), which is tentatively separated by its smaller overall size and somewhat smaller spores. Also similar are many of the species that center around *Graphis flexibilis*; a more complete discussion may be found under the latter. *Graphis flexibilis* itself is separable by its massively closed exciple and larger more protuberant ascocarps.

The *Graphis rimulosa* group differs in having smaller spores and more emergent ascocarps with no thalline margin.

SPECIMENS EXAMINED.—Morne Bruce, 400 ft, *Imshaug* 33243 (MSC); Can-Dom logging area, Newfoundland, 800 ft, *Hale* 33225 (US).

19. *Graphis lumbricina*

FIGURE 5f; PLATE 4a

Graphis lumbricina Vainio, 1899:256 [type collection: Guadeloupe, *Duss* 1036 (TUR, lectotype; FH, isotype)].

DESCRIPTION.—Thallus gray, continuous, smooth. Ascocarps at first sunken, nearly nonstriate, then striate, protuberant and large, apically black, mostly covered by a prominent thalline margin, occasionally branched, flexuose, to 5 mm long, less than 0.4 mm wide. No disc visible in surface view. Ascocarp transverse section: hymenium (100–) 170–200 μm high, I–; exciple black, closed to brown below and nearly open, lips convergent, distinctly striate. Spores 8/ascus, 10–16 locular, $12\text{--}20 \times (50\text{--}) 75\text{--}100$ (120) μm , I+ blue.

CHEMISTRY.—Norstictic acid (isotype).

HABITAT.—Rain forest, mossy forest.

DISCUSSION.—*Graphis lumbricina* is very similar to *G. flexibilis*; the latter differs in a more massively carbonized excipular base and in lacking norstictic acid. *Graphis congesta* (Fée) Mueller Argoviensis (1887) differs only in having short, congested, asteroidly-branched ascocarps. For a more complete discussion of this alliance, see *Graphis flexibilis*.

SPECIMENS EXAMINED.—Can-Dom logging area, Newfoundland, 800 ft, *Hale* 35240 (US); Fresh Water Lake, 2600–2800 ft, *Hale* 35449 (US); Trois Pitons, 29–3150 ft, *Imshaug* 33084A, 33087 (MSC).

20. *Graphis olivacea*

FIGURE 5g; PLATE 4b

Graphis olivacea Redinger, 1935:55 [type collection: Matto Grosso, Brazil, *Malme* 2267B (S, lectotype)].

DESCRIPTION.—Thallus pale olive to whitish, smooth, glossy, continuous to rather eroded, and restricted to near the ascocarps in the high elevation specimens. Ascocarps straight to flexuose, occasionally branched, apically black and striate (at least in the largest and oldest lirellae), frequently with pale streaks of thalline material between the striae, the thalline margin prominent, 1–6 mm long, slender. Disc not visible in surface view. Ascocarp transverse section: hymenium 130–200 μm high, I–; exciple black above, yellow-red to brown-red below, usually closed, lips convergent, striate. Spores 6–8/ascus, 10–18 locular, $8\text{--}10$ (–13) \times (45–) 60–90 (–125) μm , I+ blue.

CHEMISTRY.—No substances present.

HABITAT.—Wet rain forest into elfin forest, where it is very common on *Clusia venenosa* with *Phaeographis exaltata* and *P. mordenii*.

DISCUSSION.—*Graphis olivacea* is very similar to *G. flexibilis*, from which it differs in having the excipular base constructed of partially uncarbonized, yellow- to red-brown tissue. It may well be that this difference is not significant. Also quite similar is *G. rigidula*, which differs in being smaller overall. For a more complete discussion of this alliance, see *G. flexibilis*.

Graphis olivacea may prove to be a synonym of the Philippine *G. glauconigra* Vainio (1921), which appears to differ only in the smaller ascocarps and brown thallus.

SPECIMENS EXAMINED.—Can-Dom logging area, Newfoundland, 800 ft, *Hale* 35062 (US); Dleau Gommier Forest Reserve,

1200 ft, *Hale* 37988 [US]; South Chiltern Estate Road, 1500–1700 ft, *Imshaug* 32730 (MSC); Soufrière Ridge, 2200–3100 ft, *Imshaug* 33069A [MSC]; Trois Pitons, 2900–3150 ft, *Imshaug* 33089 (MSC), 4000–4672 ft, *Imshaug* 32874A [MSC], summit, *Wirth* 487, 491 (US); Morne Diablotin, 4300–4550 ft, *Imshaug* 32904A, 32909 (MSC).

21. *Graphis rigidula*

FIGURE 5h; PLATE 4c

Graphis rigidula Mueller Argoviensis, 1891:78 [type collection: San José, Costa Rica, *Pittier* 5291 (G, lectotype)].

DESCRIPTION.—Thallus white to gray, continuous, nearly glossy to minutely roughened. Ascocarps black above, flexuose, occasionally branched, covered at least halfway by the thalline margin (frequently covered nearly to the apex in the type), sometimes showing white thalline streaks between the black striae, 2–5 mm long, slender. Disc not visible in surface view. Ascocarp transverse section: hymenium 60–90 μm high, I–; exciple black, open below, lips shallowly striate, thalline margin prominent in all sections. Spores 4–6 (–8?)/ascus, 10–15 locular, 10–12 \times 50–65 μm , I+ blue.

CHEMISTRY.—No substances present (? trace of norstictic acid in the type?).

HABITAT.—Secondary forest.

DISCUSSION.—*Graphis rigidula* is extremely similar to *G. longula*; it is tentatively maintained here because of its smaller overall size and slightly smaller spores. For a more complete discussion of this species complex, see *Graphis flexibilis*.

SPECIMEN EXAMINED.—Bois Serpe, 1000 ft, *Imshaug* 32777A (MSC).

22. *Graphis rimulosa*

FIGURE 6a; PLATE 4d

Graphis rimulosa (Montagne) Trevisan, 1853:11.

Opegrapha rimulosa Montagne, 1842:271 [type collection: Guyana, *Leprieur* 200 (P, lectotype)].

DESCRIPTION.—Thallus white to gray, continuous, slightly roughened. Ascocarps raised, black, straight to flexuose, occasionally branched, clearly striate in surface view, no thalline margin evident, 1–4 mm long, slender. Ascocarp transverse section: hymenium 60–90 μm high, I–; exciple black, usually quite closed, lips convergent, striate. Spores 6–8/ascus, (8–) 10–13 locular, 9–10 \times (25–) 40–50 (–55) μm , I+ blue.

CHEMISTRY.—No substances present.

HABITAT.—Lowlands and cultivated areas.

DISCUSSION.—Very similar to *Graphis rimulosa* are the following two species.

Graphis duplicata Acharius (1814): The type material at Helsinki is externally identical to the lectotype of *G. rimulosa*. A section from the isotype at Uppsala shows an open excipular base, which appears to be the only difference between the two species.

Graphis striatula (Acharius) Sprengel (1827): The type material at Helsinki has much shorter ascocarps than *G. rimulosa* and resembles *Opegrapha* or *Melaspilea*. In addition, a section from the isotype at Uppsala shows a more or less open excipular base.

This group of species almost grades into the smallest members of the *Graphis flexibilis* complex, from which they differ in consistently lacking any thalline margin.

SPECIMENS EXAMINED.—South of Portsmouth, sea level, *Hale* 35699 (US); Roseau Valley, *Elliott* 125 (TUR); Central Forest Reserve, 1500 ft, *Imshaug* 33549A (MSC).

23. *Graphis subelegans*

FIGURE 6b; PLATE 4e

Graphis subelegans Nylander, 1891:42 [type collection: San Luis Potosí, Mexico, *Pringle* 162 (H, lectotype)].

DESCRIPTION.—Thallus usually yellow-brown, off-white in the Dominican specimen, continuous, smooth to rugose, glossy. Ascocarps usually quite raised, flexuose, rarely branched, black, obviously striate, no thalline margin present, 1–6 mm long, 0.4–0.7 mm wide. No disc visible in surface view. Ascocarp transverse section: hymenium 100–120 μm high, I–; exciple black laterally, yellow to yellow-red below, open, lips convergent, quite striate. Spores 8/ascus, 6–8 locular, 6–8 (–10) \times 25–30 μm , I+ blue.

CHEMISTRY.—No substances present.

HABITAT.—Sea level scrub (probably low elevation exposed scrub throughout its range).

DISCUSSION.—*Graphis subelegans* has been placed in synonymy (Zahlbruckner, 1923) of *G. endoxantha* Nylander (1868); however, the type of the latter (*Pancher* s.n., H) was sterile when described (and is still so) and we recommend that this name be permanently dropped.

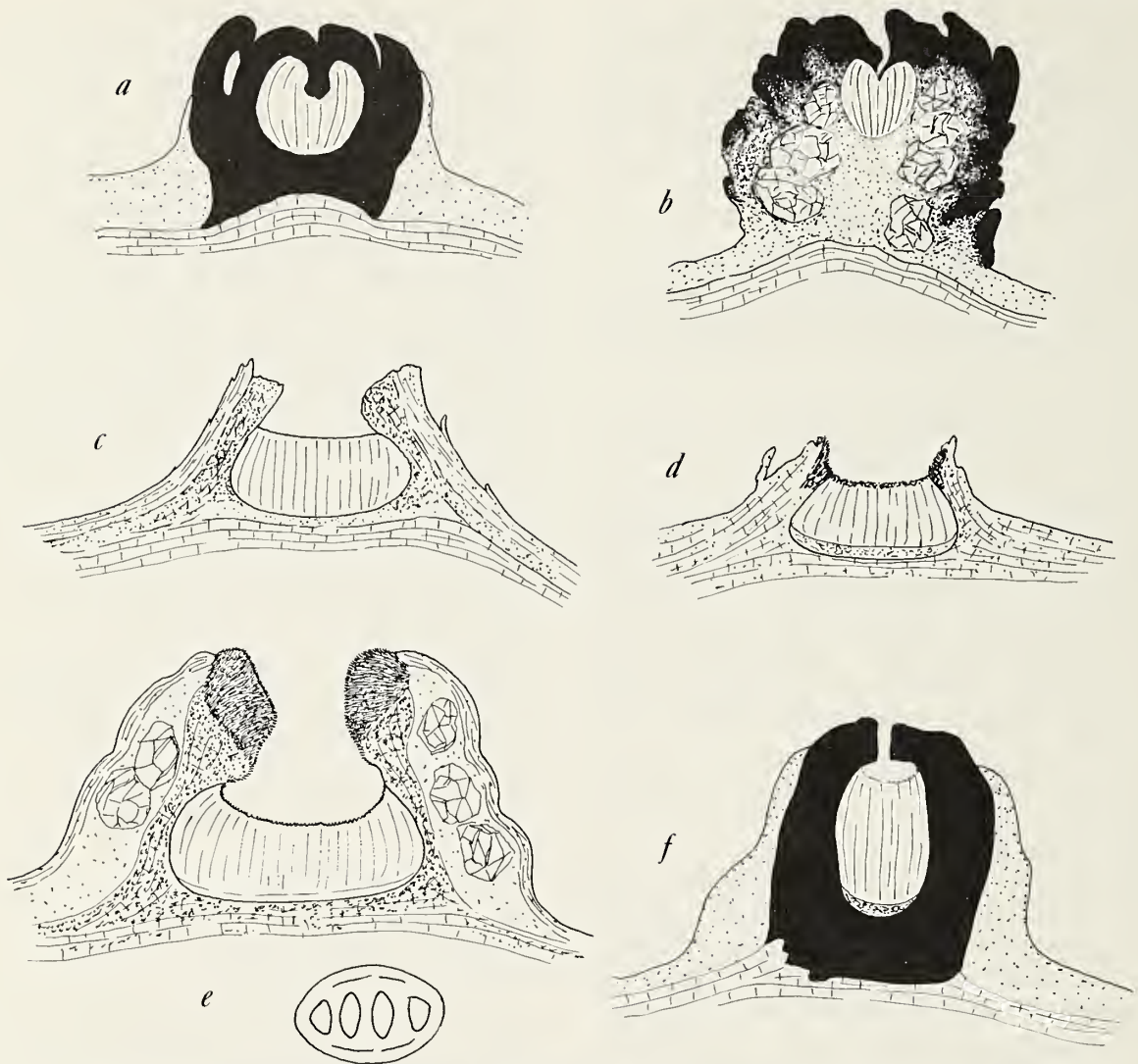


FIGURE 6.—Cross sections of apothecia of *Graphis*: a, *G. rimulosa* (lectotype in P); b, *G. subelegans* (Pringle 162); c, *G. subnitidula* (Wright 155); d, *G. tachygrapha* (Lindig 869); e, *G. triticea* (Lindig 841); f, *G. turgidula* (lectotype in BM).

There is a large group of species related to *G. subelegans*, all characterized by striate black labia embedded in basal red-yellow tissue. Most similar is probably *G. proserpens* Vainio (1909), which is smaller overall, with more sunken ascocarps. Much additional collecting is necessary to unravel this alliance.

SPECIMEN EXAMINED.—Rodney's Rock, sea level, *Hale* 35546 (US).

24. *Graphis subnitidula*

FIGURE 6c; PLATE 4f

Graphis subnitidula Nylander in Tuckerman, 1888:123 [type collection: Cuba, Wright 155 (US, lectotype; ?FH, isotype, not seen)].

Graphina subnitidula (Nylander in Tuckerman) Zahlbruckner, 1923:427.

DESCRIPTION.—Thallus brownish to greenish,

smooth, glossy, continuous, distinctly prosoplectenchymatous in section. Ascocarps fissurine, arising as a swelling which then cracks and gapes, straight, unbranched, 0.3–0.5 (–1.0) mm long. Disc just visible between the gaping lips. Ascocarp transverse section: hymenium 80–100 μm high, I–; exciple open, lips pale, convergent but exposing some epihymenium. Spores 8/ascus, 4 locular, $5 \times 8\text{--}10 \mu\text{m}$, I– or I+ faint, reddish, slow.

CHEMISTRY.—No substances present (in type; faint unknown near norstictic in the Dominican material).

HABITAT.—Upper rain forest.

DISCUSSION.—The type description of *Graphis subnitidula* cites two specimens: the Wright collection from Cuba (which is a *Graphis*, and which Nylander would have seen) and a later collection by Austin from Florida (which is a *Graphina* and probably was never seen by Nylander). Tuckerman's description clearly recognizes the mixed nature of the spores; we have chosen to follow what appears to be Nylander's original concept and consider this a *Graphis*. Zahlbruckner's transfer to *Graphina* then represents a superfluous name.

Graphis subnitidula is the smallest species yet found in the fissurine alliance; for a more complete discussion of its relatives, see *Graphis triticea*.

SPECIMEN EXAMINED.—Pont Cassé, 2200–2600 ft, *Hale*, 37676 (US).

25. *Graphis tachygrapha*

FIGURE 6d; PLATE 5a

Graphis tachygrapha Nylander, 1863:371 [type collection: Colombia, Lindig 869 (H, lectotype; FH, isotype)].

Graphis lactea var. *dominicana* Vainio, 1915:162 [type collection: Trois Pitons, Dominica, Elliott 535 (TUR, lectotype)].

Graphis timida Vainio, 1923:142 [type collection: Trinidad, Thaxter 30 (FH, lectotype)].

DESCRIPTION.—Thallus very thin, apparently endophloeodal, probably taking most of its color and texture from bark and/or epidermis. Ascocarps fissurine, beginning as cracks and finally gaping, unbranched, 0.5–1.0 mm long. Dark disc visible in gaping stages. Ascocarp transverse section: hymenium 60–90 μm high, I–, epihymenium slightly to much darker than the rest of the hymenium; exciple rudimentary below, lips convergent when young, then spreading broadly, partially or incompletely carbonized at least at the apices, sometimes

to half the height of the hymenium. Spores 8/ascus, always 4 locular, $6\text{--}9 \times 16\text{--}22 \mu\text{m}$, I– or I+ slow, reddish, pale.

CHEMISTRY.—No substances present.

HABITAT.—Elfin forest in Dominica; the type of *G. tachygrapha* is from 2600 meters in Colombia.

DISCUSSION.—Very similar to *Graphis tachygrapha* is *G. humilis*, which is tentatively separable by its I+ spores and by the much more heavily carbonized lips. For a more complete discussion of the fissurine alliance, see *Graphis triticea*.

SPECIMENS EXAMINED.—Mt. Soufrière, Elliott 1515 (TUR); Trois Pitons, summit, 4000–4672 ft, Imshaug 32862 (MSC).

26. *Graphis triticea*

FIGURE 6e; PLATE 5b

Graphis triticea Nylander, 1863:367 [type collection: Villeta, Colombia, Lindig 841 (H, lectotype; FH, isotype)].

DESCRIPTION.—Thallus tan-yellow to grayish, thick, glossy, almost always deeply cracked, cortex quite prosoplectenchymatous. Ascocarps concolorous with the thallus, arising as fissures in swollen thalline margins, sometimes barely revealing the tips of the labia and the disc (barely gaping); total raised portion 1–4 mm long, to nearly 1 mm wide. Ascocarp transverse section: hymenium 120–150 μm high, I–; exciple yellow below, open to almost closed, laterally yellow, mixed with bark cells, apically convergent to somewhat spreading, frequently with peculiar dense whitish tissue at the labial apices, the whole exciple embedded in quite swollen thalline margin tissue (“puffs”). Spores 8/ascus, always 4 locular, appearing quite rotund and almost halonate because of what appears to be a soft, hygroscopic thick outer layer, $10\text{--}15 \times 15\text{--}20 \mu\text{m}$, I– or I+ slow, reddish.

CHEMISTRY.—Stictic acid.

HABITAT.—In or just below elfin forest; probably pantropical in high altitude rain forests.

DISCUSSION.—Within the fissurine alliance, *Graphis triticea* represents the extreme of ascocarp elevation. The most similar species in the group is *G. insidiosa*, which lacks stictic acid. In addition, *G. insidiosa* usually lacks the peculiar white labial apices of most New World specimens of *G. triticea*. Most New Zealand specimens of *G. triticea* (Hayward, 1978) also lack this white tissue.

The number of names in the fissurine alliance is

large. To distinguish these generally rather inconspicuous species, we have found the following features most useful: (1) presence or absence of stictic acid; (2) thickness and degree of specialized organization of the cortex (prosoplectenchymatous versus not so); (3) swelling of thalline tissue lateral to the exciple, producing emergences in which the fissure is embedded ("puffs"); (4) degree of gaping of mature ascocarps, producing a visible disc in extreme cases (this may be a variable character and needs additional study); (5) degree of labial carbonization (rare in the group); (6) iodine reaction of spores; (7) overall size of ascocarps and size of spores (this character is useful only occasionally, as most fissurines are quite similar in this respect).

Using these seven criteria, we tentatively propose a scheme to separate many of the common fissurines (many type specimens of other names remain to be seen).

Graphis bonplandiae (Fée) Mueller Argoviensis (1887): An early fissurine name that should be permanently dropped; the type was sterile when described.

Graphis dumastii Fée (1824): No stictic acid; thallus thick, prosoplectenchymatous; no "puffing"; ascocarps gaping; no carbonization; spores I- (or reddish); size average for the alliance (nonstictic equivalent of *G. dumastioides*). *Graphis grammitica* Nylander (1866) may be synonym.

Graphis dumastioides Fink: Stictic acid; thallus thick, prosoplectenchymatous; no "puffing"; ascocarps gaping; no carbonization; spores I- (or reddish) average size for the alliance (stictic acid equivalent of *G. dumastii*).

Graphis humilis Vainio: No stictic acid; thallus thin; no "puffing"; ascocarps non-gaping; exciples carbonized; spores I+; slightly smaller ascocarps than average.

Graphis inquinata (Knight and Mitten) Hooker f. (1867): Stictic acid; thallus thick, apparently not prosoplectenchymatous; some "puffing"; ascocarps nongaping; exciple carbonized; spores I- (or reddish); average size for the alliance (rather like a carbonized equivalent of *G. triticea*).

Graphis insidiosa (Knight and Mitten) Hooker f.: No stictic acid; thallus thick, apparently prosoplectenchymatous; usually quite "puffed"; ascocarps usually not gaping; no carbonization; spores I- (or reddish); ascocarps slightly larger than average (nonstictic equivalent of *G. triticea*).

Graphis subnitidula Nylander in Tuckerman: No stictic acid; thallus thin; no "puffing"; ascocarps sometimes gaping; no carbonization; spores I- (or reddish); very small spores and ascocarps.

Graphis tachygrapha Nylander: No stictic acid; thallus thin; no "puffing"; ascocarps sometimes gaping; exciple partially carbonized; spores I-; ascocarps slightly smaller than average.

Graphis triticea Nylander: Stictic acid; thallus thick, prosoplectenchymatous; ascocarps strongly "puffed," usually not gaping; no carbonization; spores I- (or reddish); ascocarps larger than average and spores rather rotund (stictic acid equivalent of *G. insidiosa*).

Another critical early species usually placed in this alliance is *Graphis lactea* (Fée) Sprengel (1827). Preliminary examination of the type (G) indicates some doubt as to its inclusion here.

It must also be noted that a fissurine-like series exists in *Graphina*, wherein the spores frequently have only three transverse septa (as in this group) but also one or two longitudinal septa. *Graphina incrustans* appears to be a sporomorph of *Graphis dumastii*; in all probability a whole series of sporomorphs between these two alliances awaits discovery.

SPECIMENS EXAMINED.—Morne Anglais, 3000–3600 ft, *Hale* 35324, 35326B, 35377 (US); Morne Diablotin, 3200–4600 ft, *Hale* 35438, 35442 (US), 4300–4500 ft, *Imshaug* 32912 (MSC), Trois Pitons, *Elliott* 533 (TUR), 3000–4000 ft, *Imshaug* 32886 (MSC), summit, *Wirth* 482 (US); Micotrin, ca 3000 ft, *Wirth* 463B (US).

27. *Graphis turgidula*

FIGURE 6f; PLATE 5c

Graphis turgidula Mueller Argoviensis, 1895a:457 [type collection: Mauritius, s.n. (BM, lectotype)].

DESCRIPTION.—Thallus white to off-white, thick, continuous, glossy. Ascocarps prominently raised, black above, thalline margin quite pronounced, straight to more or less flexuose, rarely branched, 1–4 mm long. Ascocarp transverse section: hymenium (130–) 150–250 μ m high, I-; exciple black, massively closed below, lips convergent, intact, laterally bordered nearly to the apices by a thick thalline margin. Spores 6–8/ascus, 11–18 locular, 10–11 \times (40–) 60–90 (–105) μ m, I+ blue.

CHEMISTRY.—Stictic acid.

HABITAT.—Dominican specimen from lower montane rain forest, on *Hibiscus elatus*.

DISCUSSION.—Almost certainly synonymous with *Graphis turgidula* are *G. marginifera* Vainio (1921) and *G. tonglonensis* Vainio (1921), both from the Philippines. These two species differ only in having more exaggerated thalline margins, a feature that varies considerably even within a single thallus.

Graphis turgidula is extremely similar to *G. an-*

guilliformis, and is separable only in having stictic acid. One fairly poor specimen from Dominica (Hale 35069, Can-Dom logging area, Newfoundland) is morphologically identical to *G. turgidula* but has norstictic acid. Whether this represents a different species, or a chemically polymorphic population, remains to be seen.

SPECIMEN EXAMINED.—North of Pont Cassé, ca 1400 ft, Wirth 544B, (US).

Key to the Species of *Phaeographis*

1. Exciples with carbonized areas.
 2. Ascocarps fissure-like, inconspicuous; exciple open29. *P. arthonioides*
 2. Ascocarps robust; exciple heavily carbonized below30. *P. exaltata*
1. Exciple without carbonization.
 3. Ascocarps pink or cinnabar-red in surface view.
 4. Ascocarps cinnabar; exciples closed31. *P. haematites*
 4. Ascocarps pink; exciples rudimentary33. *P. rosea*
 3. Ascocarps white, grey or blackish in surface view.
 5. Spores over 100 μm long, usually much longer32. *P. mordenii*
 5. Spores under 35 μm long.
 6. Spores 4 locular, under 20 μm long; ascocarps usually clumped and radiately branched34. *P. cf. subtigridina*
 6. Spores 6–8 locular, over 20 μm long, ascocarps not clumped or radiately branched28. *P. albida*

28. *Phaeographis albida*

FIGURE 7a,b; PLATE 5d

Phaeographis albida (Vainio) Zahlbruckner, 1923:364.

Graphis albida Vainio, 1896:251 [type collection: Morne Anglais, Dominica, Elliott 528 (TUR, lectotype)].

DESCRIPTION.—Thallus white to off-white, continuous, matte. Ascocarps raised, unbranched to quite branched, flexuose, covered to the apex by a concolorous thalline margin, 0.5–5.0 mm long. Disc sometimes completely covered by the convergent labia, sometimes completely exposed, dark brown in surface view. Ascocarps transverse section: hymenium (70–) 80–150 μm high, I+ blue or I– (see discussion), epihymenium very dark; exciple yellow-red below and laterally, not well developed, lips convergent to quite spreading, tips brown to almost carbonized, dark portions probably derived (at least in part) by lateral compression of the epihymenium. Spores (4–) 6–8/ascus, 6–8 locular, (6–) 8–13 \times 20–35 μm , frequently halonate after release, I+ blue (in the type some cells appearing very irregularly muriform).

CHEMISTRY.—No substances present.

HABITAT.—Elfin forest and high altitude rain forest.

DISCUSSION.—*Phaeographis albida* is a distinct species, apparently endemic to Dominica. The Hale and Imshaug collections have ascocarps with spreading labia and much more disc exposed than the type; we have found, however, that this character is very variable, even within a single thallus, in species with uncarbonized exciples. A very good parallel example is illustrated for *Graphina colliculosa*.

This is the only species known to us with a variable iodine reaction of the hymenium.

Extremely similar to *P. albida* is *Phaeographina oscitans*; the latter can be distinguished only by the spores, the consistently I– hymenium, and the presence of stictic acid.

SPECIMENS EXAMINED.—Fresh Water Lake, 2600–2800 ft, Hale 35453 (US); Morne Diablotin, 3500–4300 ft, Imshaug 32936 P.P. (MSC).

29. *Phaeographis arthonioides*

FIGURE 7c; PLATE 5c

Phaeographis arthonioides (Vainio) Zahlbruckner, 1923:364.

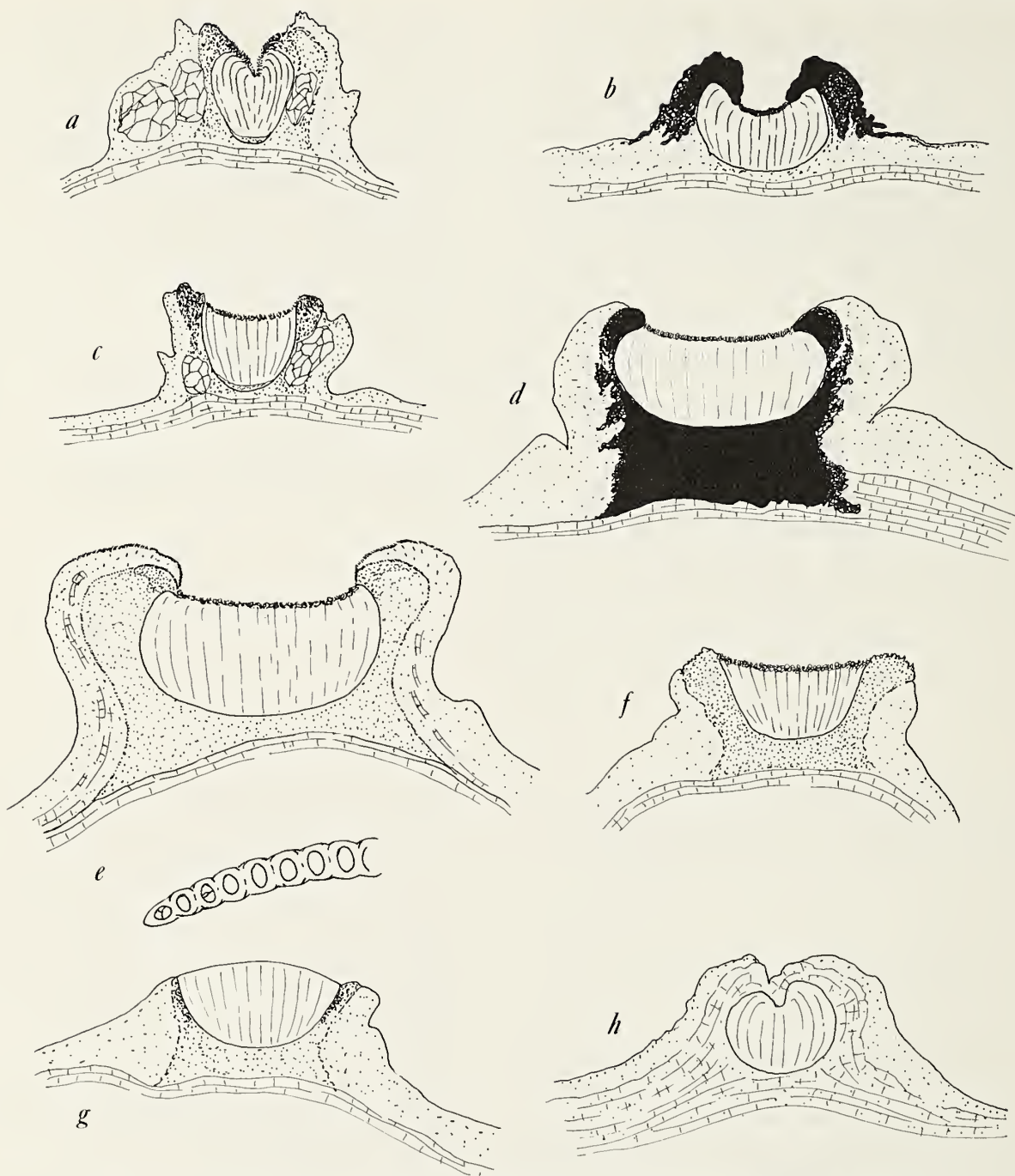


FIGURE 7.—Cross sections of apothecia of *Phaeographis*: a, *P. albida* (Elliott 528); b, *P. albida* (Hale 35453); c, *P. arthonioides* (Raunkiaer 548); d, *P. exaltata* (Elliott 1301); e, *P. mordenii* (Hale 35071); f, *P. haematites* (Hale 38013); g, *P. cf. subtigrina* (Wirth 444); h, *P. rosea* (Elliott 523).

Graphis arthonioides Vainio, 1915:155 [type collection: St. Croix, *Raunkiaer* 548 (FH, isotype)].

Phaeographis sexloculata Fink, 1927:215 [type collection: Puerto Rico, *Fink* 1436 (MICH, lectotype)].

DESCRIPTION.—Thallus gray to whitish, continuous, glossy, rather thin. Ascocarps fissurine, barely raised, margins blackish to black, mostly unbranched, straight to somewhat flexuose, usually 1 mm or less long. Disc usually not visible in surface view. Ascocarp transverse section: hymenium 65–70 μm high, I–, epihymenium dark; exciple rudimentary below, lips more or less convergent, irregularly carbonized at least apically, frequently to the base of the hymenium. Spores 8/ascus, 6–8 locular, 7–10 \times 19–26 μm , I– or I+ slow, reddish.

CHEMISTRY.—Isotype of *P. arthonioides* has a faint unknown; lectotype of *P. sexloculata* is P–, too small for adequate TLC; Dominican specimen contains no substances.

HABITAT.—Lowlands in exposed or cultivated areas.

DISCUSSION.—Extremely similar to *Phaeographis arthonioides* is *P. decipiens* (Fée) Mueller Argoviensis (1887), also from the Caribbean; the latter differs only in having stictic acid. Differing only in spores is *Graphis humilis* Vainio.

SPECIMEN EXAMINED.—East of Pointe Michel, 200 ft, *Imshaug* 33128 (MSC).

30. *Phaeographis exaltata*

FIGURE 7d; PLATES 5f, 6a

Phaeographis exaltata (Montagne and van den Bosch) Mueller Argoviensis, 1882:336.

Lecanactis exaltata Montagne and van den Bosch, 1855:475 [type collection: Java, *Junghuhn* s.n. (L, lectotype)].

DESCRIPTION.—Thallus nearly white to gray, thick, usually glossy, continuous. Ascocarps very prominent, from *Sarcographa*-like and circular to elongate and flexuose (on one thallus), thalline margin very prominent, from 1 \times 1 mm to 1 \times 6 mm. Disc wide, black to gray-pruinose. Ascocarp transverse section: hymenium 120–200 μm high, I–, epihymenium blackened; exciple black, heavily closed below, lips usually quite spreading, intact, frequently incompletely carbonized. Spores 8/ascus, 6–8 locular, 7–11 \times 20–30 μm , I– or I+ faint, slow, reddish.

CHEMISTRY.—See “Discussion.”

HABITAT.—Upper montane and elfin forest. One of the three major graphids on elfin forest *Clusia venenosa* (with *Graphis olivacea* and *Phaeographis mordenii*).

DISCUSSION.—*Phaeographis exaltata* is a widespread, common pantropical species of high altitude rain forests. The large size, distinctive appearance, and heavily carbonized exciple render it unlikely to be confused with any other species of *Phaeographis*. Individual specimens (and frequently parts of a single specimen) can mimic *Sarcographa* closely; the only consistent difference is the lack of cracking and partitioning of the disc so common in *Sarcographa*.

Partially because of the distinctive morphology, we find it difficult to split *P. exaltata* into two chemical species. The vast majority of the Paleotropic specimens (including the type) have no lichen acids; the vast majority of Neotropic specimens have at least one of the three “quintaria” unknowns. Even within the relatively small area of Dominica both chemical forms can be found.

As *P. exaltata* is both common and fairly well represented in herbaria, it would seem to be an excellent subject for a future study of chemical variation in a crustose species.

SPECIMENS EXAMINED.—Can-Dom logging area, Brantridge Estate, 1700 ft, *Hale* 35301, 35321 (US); Can-Dom logging area, Ponte Cassé, 2000 ft, *Hale* 35009, 35091, 35100, 35115, 35116 (US); Boiling Lake, 2400–3000 ft, *Hale* 35622A (US); Morne Anglais, 3000–3600 ft, *Hale* 35322 (US); Trois Pitons, 3000–4000 ft, *Imshaug* 32883, 32888 (MSC), summit, *Wirth* 480, 483 (US); Morne Diablotin, 3500–4300 ft, *Imshaug* 32934 (MSC), 3200–4600 ft, *Hale* 35323, 35445 (US); Prince Rupert, *Elliott* 1307 (TUR).

31. *Phaeographis haematites*

FIGURE 7f; PLATE 6b

Phaeographis haematites (Fée) Mueller Argoviensis, 1882:384. *Graphis haematites* Fée, 1824:45 [type collection: South America, s.n. (G, lectotype)].

DESCRIPTION.—Thallus tan to pale brown, continuous, smooth to matte. Ascocarps raised, prominent, occasionally branched, usually quite sinuous, thalline margin very prominent, usually covering the ascocarp to the apex (but frequently separated from the disc and labia by a distinct crack), up to 15 mm long, slender. Disc (and labial tips) deep to bright cinnabar-orange, disc quite obvious in sur-

face view. Ascocarp transverse section: hymenium 80–100 μm high, I–; exciple red, uncarbonized, more or less closed, the pigment soluble in Hoyer's medium, labia more or less spreading, somewhat thickened apically. Spores 8/ascus, 6–10 locular, 9–11 \times 21–35 μm , I–.

CHEMISTRY.—No substances present except for the red pigment.

HABITAT.—Rain forest in Dominica; probably from lowland scrub to high rain forest elsewhere in its range.

DISCUSSION.—*Phaeographis cinnabarina* (Fée) Mueller Argoviensis (1887) is the only species likely to be confused with *P. haematites*. The former can easily be distinguished by its thinner, duller ascocarps, with a brownish rudimentary exciple, and the much smaller hymenium with much darkened epihymenium. Somewhat similar is *Phaeographina chrysocarpa* (Raddi) Redinger (1933), which differs in the spores and in the heavily carbonized exciple.

SPECIMEN EXAMINED.—Dleau Gommier Forest Reserve, 1200 ft, Hale 38013 (US).

32. *Phaeographis mordenii*, new species

FIGURE 7e; PLATE 6c

DESCRIPTION.—Thallus continuus, laevis vel ruguloso-inaequalis. Apothecia sessilia, rotunda vel lirellina, simplicia, recta, 2–8 longa, ca. 1 mm lata, disco dilatato, primum pallido, dein nigricante, pruinoso. Excipulum subintegrum, flavum vel rufo-ferrugineum, labiis integris, divergentibus; hymenium inspersum, 200–250 μm altum, I–. Asci 6–8 spori, sporae fuscescentes, 30–40 (–50) loculares, 12–17 \times 120–220 μm , in mentem revocans sporae *Conotremae*, I+ rufo-fuscae.

Thallus light gray and glossy near the apothecia, white and matte where more exposed, continuous, distinctly rugulose in spots. Ascocarps prominently raised, nearly round to irregular to elongate, rarely branched, with a prominent thalline margin, 2–8 mm long, ca. 1 mm wide. Disc very broad, initially concolorous with the thallus, then dark blackish-gray and pruinose. Ascocarp transverse section: hymenium 200–250 μm high, heavily inspersed and beaded, epihymenium darkened, I–; exciple closed to nearly open, reddish yellow, labia intact, divergent, covered by the thalline margin. Spores 6–8/ascus, brown, very long and slender, 30–40 (–50)

locular, 12–17 \times 120–220 μm , occasionally with irregular biocellations in the end chambers, chamber walls frequently thickened, reminiscent of *Conotrema* spores, I+ slow, eventually dark red-brown.

CHEMISTRY.—No substances present.

HOLOTYPE.—Mossy and elfin forest, trail to summit of Morne Diablotin, Dominica, 3200–4600 feet, Hale 35071 (US).

DISCUSSION.—*Phaeographis mordenii* is one of the three characteristic and abundant graphids on *Clusia venenosa* in the elfin forest. It is quite distinct in its large size and enormous, thick-walled spores; there would seem to be no closely related species.

Occasionally, some spores will show biocellate ends, similar to those of *Graphina vestoides*; however, these extra locules are irregular and seem to represent disintegration of cell contents rather than a submuriform condition.

SPECIMENS EXAMINED.—Morne Diablotin, 3500–4300 ft, Imshaug 32922, 32945A (MSC); Morne Trois Pitons, 3000–4000 ft, Imshaug 32884 (MSC), summit, on *Clusia venenosa*, Wirth 479, 481, 484, 485, 486 (US).

33. *Phaeographis rosea*

FIGURE 7h; PLATE 6d

Phaeographis rosea (Vainio) Zahlbruckner, 1923:385.

Graphis rosea Vainio, 1896:259 [type collection: Morne Anglais, Dominica, Elliott 523 (TUR, lectotype)].

DESCRIPTION.—Thallus tan, continuous, smooth and shining. Ascocarps barely emergent, rather fissurine, occasionally branched, flexuose, the margins distinctly stained rose-pink, 5–15 mm long, slender. Disc not visible in surface view. Ascocarp transverse section: hymenium 140–160 μm high, I–; exciple rudimentary, labia convergent, brownish above. Spores 8/ascus, always 4 locular, 9–12 \times (13–) 18–25 μm , I+ blue.

CHEMISTRY.—No substances present.

HABITAT.—Upper montane forest.

DISCUSSION.—*Phaeographis rosea* is known only from the type collection. The rose-pink pigmentation that renders this species so distinct is apparently a normal condition; occasionally, some graphids will show discolored, reddish areas on thalli of normally unpigmented species (see *Gra-*

phina dimidiata for a Dominican example). The color in *P. rosea*, however, is restricted to the ascocarp margins, and appears to be normal.

34. *Phaeographis* cf. *subtigrina*

FIGURE 7g; PLATE 6e

Phaeographis subtigrina (Vainio) Zahlbruckner, 1923:387.
Graphis subtigrina Vainio, 1907:177 [type collection: Koh Chang, Gulf of Siam, *Schmidt* XXI (TUR, lectotype)].

DESCRIPTION.—Thallus thin, off-white, continuous, matte. Ascocarps usually clumped, commonly radiately branched, forming clusters to 2 mm in diameter, flush, thalline margin frequently separating from the thallus. Disc broad, gray, lightly but distinctly pruinose. Ascocarp transverse section: hymenium 115 μ m high (Dominican specimens; no measurement for the type), I–; exciple pale below, closed to nearly open, lips darker but not carbonized, intact, divergent. Spores 8/ascus, thick-walled, 4 locular, 4–6 \times 10–17 μ m, I–.

CHEMISTRY.—Norstictic acid only (type); norstictic and stictic acid (Dominican specimens).

HABITAT.—One Dominican specimen from sea-level, the other from upland rain forest. Apparently of great ecological amplitude.

DISCUSSION.—*Phaeographis subtigrina* has been reported (Vainio, 1915) from Guadelope, but we have not seen these specimens. The Dominican material differs from the type primarily in the chemistry.

As in many species of *Phaeographis*, the ascocarp form in *P. subtigrina* varies greatly within the same thallus. In the Dominican specimens these structures vary from very narrow, heavily branched, and clumped to quite broad, barely branched, and hardly clumped.

Quite similar to *P. subtigrina* is *P. dimorpha* (Nylander) Zahlbruckner (1923), which differs in having a more prominent margin and more raised ascocarps.

SPECIMENS EXAMINED.—Roseau Botanic Garden, Wirth 444 (US); Emerald Pool, Wirth 505 (US).

Key to the Species of *Graphina*

1. Exciples distinctly carbonized.
 2. Disc broad and obvious in surface view, labia quite divergent.
 3. Spores with broad persistent colloidal layer; ascocarps flush with thalline surface41. *G. collospora*
 3. Spores without colloidal layer; ascocarps more or less raised.
 4. Spores 1/ascus; protocetraric acid present52. *G. platyleuca*
 4. Spores more than 1/ascus, some darkening; no substances present63. *Phaeographina* cf. *difformis*
 2. Disc narrow, not prominent in surface view, labia more or less convergent.
 5. Ascocarps with powdery white covering, easily rubbed to expose the black exciple.
 6. Spores under 20 μ m long; salazinic acid present50. *G. marcescens*
 6. Spores over 40 μ m long; stictic acid present57. *G. triphoroides*
 5. Ascocarps without a powdery white covering.
 7. Labia entire or nearly so.
 8. Exciple carbonization limited to labial apices (upper 1/2 or less of total exciple height43. *G. dimidiata*
 8. Exciple carbonization extending to base of hymenium or beyond.
 9. Ascocarps *Opregrapha*-like, 1–2 mm long, without a thalline margin51. *G. nuda*
 9. Ascocarps elongate, flexuose, with a thalline margin.
 10. Spores less than 61 μ m long.
 11. Norstictic acid present; mature spores 8/ascus54. *G. pseudoanaloga*
 11. No substances present; mature spores usually 4–6/ascus53. *G. plurispora*

10. Spores over 85 μm long.
 12. Only the ends of the spores muriform58. *G. vestitoides*
 12. Entire spore densely muriform.
 13. Ascocarps under 0.5 mm wide; hymenium under 250 μm high.35. *G. acharii*
 13. Ascocarps massive, usually 1 mm wide; hymenium over 350 μm high46. *G. illinata*
7. Labia striate.
 14. Exciple yellow to yellow-brown laterally, more or less open37. *G. antillarum*
 14. Exciple without yellowish areas, closed or nearly so.
 15. Spores under 61 μm long.
 16. Norstictic acid present; mature spores 8/ascus54. *G. pseudoanaloga*
 16. No substances present; mature spores usually 4-6/ascus53. *G. plurispora*
 15. Spores over 64 μm long.
 17. Only ends of spores muriform58. *G. vestitoides*
 17. Entire spore densely muriform.
 18. Exciple base irregularly carbonized; spores always 1/ascus.....49. *G. macella*
 18. Exciple base usually evenly carbonized; spores usually 4/ascus35. *G. acharii*
1. Exciples totally uncarbonized.
 19. Apothecia fissurine, i.e., originating as a crack, the disc usually concealed by or sunken between the narrow to gaping fissure walls.
 20. Spores 1/ascus, over 50 μm long48. *G. insculpta*
 20. Spores 6-8/ascus, under 50 μm long.
 21. Thallus prosoplectenchymatous47. *G. incrustans*
 21. Thallus not prosoplectenchymatous.
 22. Psoromic acid present42. *G. columbina*
 22. No substances present36. *G. cf. adscribens*
 19. Ascocarps not fissurine.
 23. Disc broad, easily seen in surface view.
 24. Disc reddish; spores under 17 μm long; salazinic acid present40. *G. colliculosa*
 24. Disc whitish, gray to greenish; spores over 17 μm long; salazinic acid absent.
 25. Spores 17-28 μm long; norstictic acid present56. *G. suberythrella*
 25. Spores 50-150 μm long; "quintaria" unknowns present59. *G. virginea*
 23. Disc narrow, not prominent in surface view.
 26. Margins of ascocarps distinctly reddish to pinkish brown in surface view, at least in upper portions.
 27. Spores 1/ascus, over 80 μm long39. *G. chlorocarpa*
 27. Spores 2-8/ascus, under 75 μm long.
 28. Norstictic acid present; exciples with internal striae only44. *G. dispersa*
 28. No substances present; internal striae absent.
 29. Mature spores 2-4/ascus, over 35 μm long; labia slightly striate55. *G. rufopallida*
 29. Mature spores 8/ascus, less than 18 μm long; labia entire38. *G. carneoviridis*
 26. Margins of ascocarps tan, white, or greenish.
 30. Spores less than 17 μm long; salazinic acid present.....40. *G. colliculosa*
 30. Spores more than 40 μm long; salazinic acid absent.
 31. Ascocarps always massive and protuberant; hymenium over 200 μm high; I-; no substances present.45. *G. frumentaria*
 31. Ascocarps rarely protuberant, never massive; hymenium less than 200 μm high, at least the epihymenium I+ blue; "quintaria" unknowns present59. *G. virginea*

35. *Graphina acharii*

FIGURE 8a; PLATE 6f

Graphina acharii (Fée) Mueller Argoviensis, 1887:38.

Graphis acharii Fée, 1824:39 [type collection: South America, s.n. (G. lectotype)].

Graphis inturgescens Krempelhuber, 1876:383 [type collection: Brazil, Glaziov 6286 (BM, lectotype; M, isotype)].

Graphina inturgescens (Krempelhuber) Mueller Argoviensis, 1888a:545.

DESCRIPTION.—Thallus gray to off-white, thick, continuous to cracked. Ascocarps large, strongly raised, black above, straight to flexuose, occasionally branched, covered nearly to the tops by a prominent thalline margin, 1–6 mm long. Disc not visible in surface view. Ascocarp transverse section: hymenium 150–200 μm high, proportionately small, I–; exciple black, massively closed, labia convergent, nearly entire to crenate to distinctly striate (often within a single ascocarp). Spores (in the type of *G. acharii*) usually 4/ascus but occasionally one or three (and rarely six), densely muriform, $18\text{--}25 \times 95\text{--}170 \mu\text{m}$, I+ blue.

CHEMISTRY.—No substances present.

HABITAT.—Secondary forest (Dominica).

DISCUSSION.—According to Mueller Argoviensis (1887), the spores in the type of *G. acharii* have biocellate ends; however, we have been able to find only densely muriform spores in this same material. In an earlier treatment of this species (Wirth and Hale, 1963), we had not seen the type, and followed Mueller in including specimens with biocellate spores in *G. acharii*. Although additional collections may prove these spore variants to be part of the same continuum, we are presently restricting the name *G. acharii* to those forms with densely muriform spores only. Those specimens with biocellate spores can be referred to *G. vestitoides* (p. 44).

The ascocarps in *G. acharii* vary from nearly oryzaeform to quite long, frequently within the same specimen. Also very variable is the number of spores per ascus, and the degree of striation of the labia. The subentire labia characteristic of *G. inturgescens* can frequently be found on the same thallus with the heavily striate labia of typical *G. acharii*.

This species is extremely common throughout the Neotropics; a sporomorph is *Graphis flexibilis*.

Somewhat similar among the Dominican *Gra-*

phina species is *G. macella*, which differs in being smaller overall and in having an irregularly carbonized excipular base.

SPECIMEN EXAMINED.—Syndicate Estate, 1800 ft, Hale 35555 (US).

36. *Graphina* cf. *adscribens*

FIGURE 8b; PLATE 7a

Graphina adscribens (Nylander) Mueller Argoviensis, 1892a:284.

Graphis adscribens Nylander, 1868:177 [type collection: Lifu, New Caledonia, Thiebaut s.n. (H, lectotype)].

DESCRIPTION.—Thallus white, thin, continuous to cracked. Ascocarps very inconspicuous in the Dominican material and in the type photographs, fissurine, slightly mealy in the Dominican specimen, concolorous with the thallus (at least in the Dominican specimen), less than 1 mm long. Disc not visible in surface view. Ascocarp transverse section: hymenium 100–120 μm high, (I– Dominican specimen); exciple rudimentary in the Dominican material, apparently slightly reddish in the type, lips convergent, intact. Spores 8/ascus, muriform $8\text{--}9 \times 21\text{--}27 \mu\text{m}$ (type), $9\text{--}10 \times 23\text{--}40$ (Dominica), I– in type (fide Nylander), I+ reddish, slow in the Dominican material.

CHEMISTRY.—No substances present (both specimens).

HABITAT.—On *Cocos* at beach (Dominica only).

DISCUSSION.—This tentative identification is based on a black and white photograph of the lectotype (which is a very small specimen) and a sketch of the excipular cross-section of the type. According to both Nylander and Mueller, the type is reminiscent of *Graphina chlorocarpa* and *Graphis grammitis*, both of which have reddish ascocarps in surface view. As the Dominican specimen is uniformly pale, the identification must remain tentative until the type can be examined.

SPECIMEN EXAMINED.—Ans du Me, Wirth 519 (US).

37. *Graphina antillarum*

FIGURE 8c; PLATE 7b

Graphina antillarum (Vainio) Zahlbruckner, 1923:398.

Graphis antillarum Vainio, 1899:255 [type collections, Guadeloupe, Duss 540 (FH, isotype)].

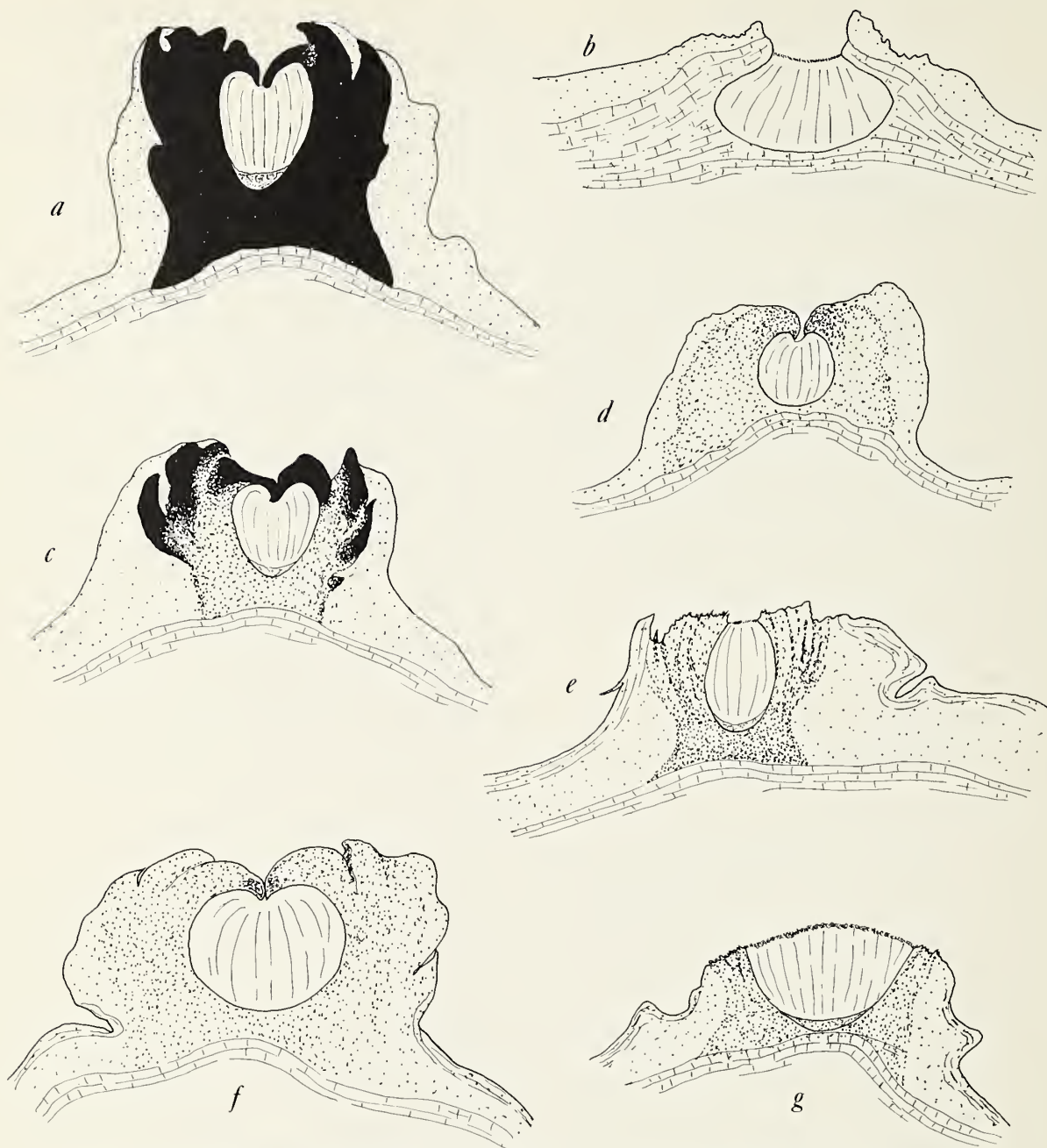


FIGURE 8.—Cross sections of apothecia of *Graphina*: a, *G. acharii* (lectotype in G); b, *G. cf. adscibens* (Wirth 519); c, *G. antillarum* (Duss s.n.); d, *G. carneoviridis* (Hale 37642); e, *G. chlorocarpa* (lectotype in G); f, *G. colliculosa* (lectotype of *G. eugeniae*, Merrill 3471); g, *G. colliculosa* (lectotype in PC).

Graphis acuminata Vainio, 1915:147 [type collection: St. Jan, Raunkiaer 437 (TUR, lectotype)].

Graphis platycarpoides Vainio, 1915:145 [type collection, Guadeloupe, Duss 1198 (TUR, lectotype)].

Graphina acuminata (Vainio) Zahlbruckner, 1923:393.

Graphina platycarpoides (Vainio) Zahlbruckner, 1923:419.

Graphina sulcata Fink, 1927:217 [type collection: Puerto Rico, Fink 659 (MICH, lectotype)].

DESCRIPTION.—Thallus gray to white, continuous, matte. Ascocarps nearly flush to partially emergent, black, commonly branched and flexuose, thalline

margin absent or nearly so, 5–6 mm long, slender. Ascocarp transverse section: hymenium 80–100 (–120) μm high, I–, exciple black laterally, yellow to yellow-brown below, more or less open, labia convergent, barely to quite strongly striate. Spores (1–) 2–4 (–6)/ascus, distinctly muriform, 15–22 \times 28–46 (–60) μm , I+ blue.

CHEMISTRY.—Norstictic acid.

HABITAT.—Lowland scrub forest and higher altitude cultivated areas and road cuts.

DISCUSSION.—Among the *Graphina* species with carbonized, striate, dimidiate exciples, *G. antillarum* is fairly distinct by virtue of its 2–4 small, rotund spores per ascus, and the presence of norstictic acid. There are, however, several other species that are extremely similar and may prove to be conspecific:

Graphina bipartita Mueller Argoviensis (1888c) differs in having a thin thalline layer over the ascocarps and in having only the very tips of the labia carbonized.

Graphina deserpens (Vainio) Zahlbruckner (1923) differs in having 8 spores per ascus and stictic acid. It is probably a synonym of *G. parilis*, below.

Graphina elongata (Vainio) Zahlbruckner (1923) differs in having both stictic acid and norstictic acid, more dendritically branched apothecia, and no basal yellow area in the exciple.

Graphina parilis (Krempelhuber) Mueller Argoviensis (1892b) differs in having stictic acid and 8 spores per ascus.

Most of the Dominican specimens fit comfortably within the boundaries defined here for *G. antillarum*. One, however (Wirth 544c), has the brown exciple base of *G. elongata* but lacks the stictic acid of *G. elongata*.

SPECIMENS EXAMINED.—Prince Rupert Bay, *Imshaug* 33529A (MSC); Brookhill Estate, 100–150 ft, *Imshaug* 33307A (MSC); Roseau Botanic Garden, 100 ft *Wirth* 445 (US); north of Bioche, 200 ft, *Hale* 35745; South Chiltern Estate, 1300 ft, *Imshaug* 33050, 33036 (MSC); near Pont Cassé, 1400 ft, *Wirth* 544c (US).

38. *Graphina carneoviridis*, new species

FIGURE 8d; PLATE 7c

DESCRIPTION.—Thallus continuus, laevis, stratum corticale prosoplectenchymatum. Apothecia sessilia, recta vel flexuosa, 1–2 (–3) mm longa. Excipulum dimidiatum, rufo-fuscum, labiis convergentibus, in-

tegris vel indistincte incis; hymenium 75 μm altum, I–. Asci 8 spori; sporae decolores, murales, loculis horizontalibus 3, locus transversis 2, 10–12 \times 15–17 μm , I+ coeruleae.

Thallus greenish, continuous to somewhat cracked, glossy, prosoplectenchymatous. Ascocarps raised, occasionally branched, straight to flexuose, pink-brown above, laterally bounded by a green thalline margin, 1–2 (–3) mm long, slender. Disc not visible in surface view. Ascocarp transverse section: hymenium 75 μm high, I–; exciple reddish-brown, open below, labia convergent, intact to barely striate. Spores 8/ascus, 3 \times 2 locular, 10–12 \times 15–17 μm , I+ blue.

CHEMISTRY.—No substances present.

HOLOTYPE.—Mixed disturbed and primary rain forest, trail from Brigantin through Middleham Estate toward Morne Trois Pitons, Dominica, elevation 2200–2600 feet, *Hale* 37642 (US).

DISCUSSION.—*Graphina carneoviridis* is externally rather similar to *Graphina dispersa*, from which it differs in having smaller spores, a more open exciple with nearly intact labia, a prosoplectenchymatous cortex, and in a different chemistry.

39. *Graphina chlorocarpa*

FIGURE 8e; PLATE 7d

Graphina chlorocarpa (Fée) Mueller Argoviensis, 1887:44.

Graphis chlorocarpa Fée, 1824:47 [type collection: *Peru*. s.n. (G, lectotype)].

Graphina balbisii var. *monospora* Redinger, 1933:61 [type collection, *Malme* 494 (S, lectotype; FH, isotype)].

DESCRIPTION.—Thallus tan to grey-green, continuous, glossy, smooth to slightly rugose. Ascocarps usually raised (nearly flush when young), straight to quite flexuose, usually unbranched, concolorous with the thallus except (usually) for the disc, which is pale orange-brown, 1–5 mm long, about 0.5 mm wide. Ascocarp transverse section: hymenium 120–180 μm high, I–; exciple yellow-brown to red-brown, open below, labia convergent, lightly striate, the tips of the striae sometimes slightly darkened. Spores 1/ascus, densely muriform, 24–40 \times 80–130 μm , I+ blue.

CHEMISTRY.—Both types and most specimens: no substances present. A few Dominican specimens with unknown substances.

HABITAT.—All fertile specimens from rain forest; sterile material (see discussion) from sea level and

mid altitude cultivated areas.

DISCUSSION.—The only neotropical *Graphina* species likely to be confused with *G. chlorocarpa* is *G. balbisii* (Feé) Mueller Argoviensis. Both these species share the distinctive orange-brown disc area and the striate reddish exciple; the only difference lies in the number of spores per ascus. In *G. chlorocarpa* the asci are always monosporous; in *G. balbisii* the asci usually contain 3–4 slightly smaller spores, occasionally 6 or 2, but never only one. As yet, we have seen no specimens that bridge the rather small gap between these two species.

Without spores, it is not possible to be sure which of these two species is in hand. All the fertile Dominican material referable to *G. chlorocarpa* is from rain forest; however, four additional specimens from cultivated areas (*Imshaug* 33024, 33417, 33424, *Wirth* 446) are sterile and may be either of the two species. No fertile material of *G. balbisii* has yet been identified from the Island.

SPECIMENS EXAMINED.—Near Laudat, 800 ft, *Hale* 35797 (US); Can-Dom logging area, Pont Cassé, 2000 ft, *Hale* 35097, 35129 (US); Ridgefield Estate, 1100–1200 ft, *Imshaug* 33417, 33424 (MSC, both sterile); South Chiltern Estate, 1300 ft, *Imshaug* 33024 (MSC, sterile); Roseau Botanic Garden, 100 ft, *Wirth* 446 (US, sterile).

40. *Graphina colliculosa*

FIGURES 8f,g; PLATE 7e

Graphina colliculosa (Montagne) Hale, 1976:156.

Sclerophyton colliculosum Montagne, 1851:61 [type collection:

Guyana, *Leprieur* 1406 (P, lectotype; BM, isotype)].

Graphis intortula Stirton, 1881:186 [type collection: Assam, s.n. (BM, lectotype)].

Graphis eugeniae Vainio, 1921:262 [type collection: Philippines, *Merrill* 3971 (TUR, lectotype; FH, isotype)].

Graphis colliculosa (Montagne) Zahlbruckner, 1923:299.

Graphina intortula (Stirton) Zahlbruckner, 1923:411.

Graphina aibonitensis Fink, 1927:215 [type collection: Puerto Rico, *Fink* 2017 (MICH, lectotype)].

DESCRIPTION.—Thallus gray to pale tan to faintly greenish, smooth, glossy, continuous, thick, the upper layer compacted and prosoplectenchymatous in section. Ascocarps raised, sinuous, commonly branched, to 30 mm long, slender. Disc sometimes prominently displayed as a red-brown line in surface view, sometimes completely covered by the concolorous thalline margin. Ascocarp transverse section: hymenium 80–100 μ m high, I–, epihymenium

darkened; exciple rather ill-defined, yellow to reddish-yellow, usually closed below, labia quite convergent to quite divergent, more or less intact or having the appearance of internal striae. Spores 8/ascus, 4×1 –2 locular, 5 – 7×11 –16 μ m, I+ blue.

CHEMISTRY.—Salazinic acid.

HABITAT.—Rain forest canopy in Dominica; elsewhere found in both rain forest and secondary forest.

DISCUSSION.—*Graphina colliculosa* is an extremely vigorous, pantropical species; we have seen specimens from much of the Caribbean (Cuba, Puerto Rico, St. Vincent, Grenada, Trinidad, St. Lucia), Panama, Guayana, Tahiti, Fiji, Assam, and the Philippines.

As in many species with totally uncarbonized exciples, the degree of labial divergence is quite variable (see *Phaeographis albida* for a parallel condition). The taxa listed as synonyms differ from each other primarily in the extent to which the red-brown disc is exposed; as complete exposure and complete concealment can be found within a single thallus, this character seems clearly useless to distinguish species.

A second feature that is quite variable in many species with uncarbonized labia is the presence of "internal" striae, i.e., dark lines within the lips. These darkened masses of cells seem to arise with age, by lateral compaction of old hymenium. The type of *G. aibonitensis* (Figure 9a) is a good example of the extreme of this condition. Note also the very thick basal closure of the exciple, which seems also to be correlated with age.

Chemically, *G. colliculosa* is unlikely to be confused with any other species, as salazinic acid is quite rare in the family. However, several other species are quite similar in morphology, as follows.

Graphina erythrella (Montagne) Zahlbruckner (1923) is distinguished by having norstictic acid, larger spores, and somewhat shorter, more raised ascocarps. Some of the sterile, norstictic acid-containing syntypes of *G. eugeniae* (*MacGregor* 41315, *Elmer* 15077) may be referable to this species.

Graphina riopiedrensis Fink (1927) differs only in the somewhat larger spores and in having stictic acid.

SPECIMENS EXAMINED.—Castle Bruce Road, 1000 ft, *Hale* 38177 (US); Can-Dom logging area, Dleau Gommier, 1600–1700 ft, *Hale* 35175 (US); Soufrière Ridge, 2200–3100 ft, *Imshaug* 33068 (MSC).

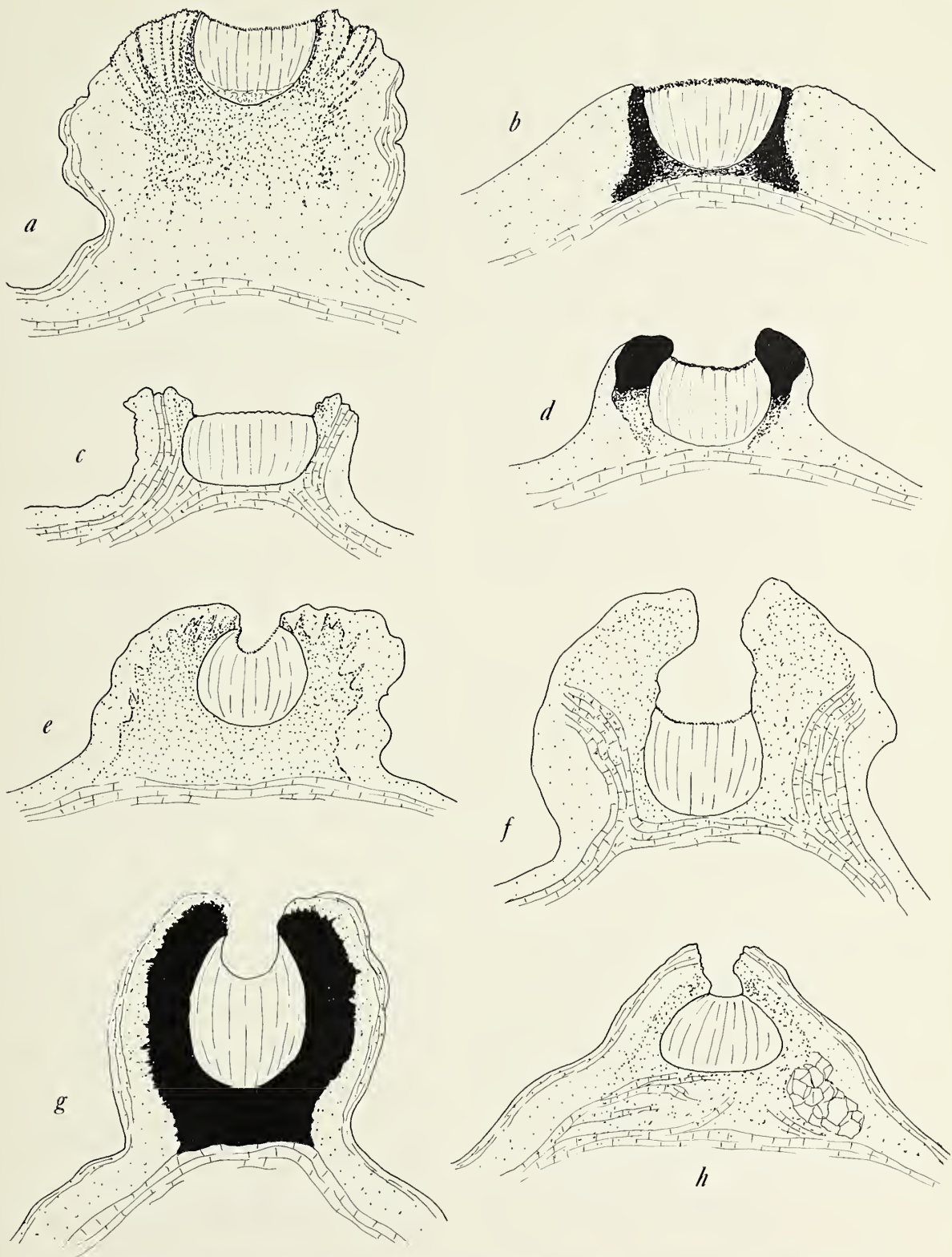


FIGURE 9.—Cross sections of apothecia of *Graphina*: a, *G. colliculosa* (lectotype of *G. aibonitensis* Fink); b, *G. collospora* (Boergesen s.n.); c, *G. columbina* (Beaumont s.n.); d, *G. dimidiata* (Vainio 332); e, *G. dispersa* (Malme 2038B); f, *G. frumentaria* (lectotype in G); g, *G. illinata* (lectotype in M); h, *G. incrustans* (lectotype in G).

41. *Graphina collospora*

FIGURE 9b; PLATE 7f

Graphina collospora (Vainio) Zahlbruckner, 1923:402.*Graphis collospora* Vainio, 1915:153 [type collection: Mt. Eagles, St. Croix, Boergesen s.n. (TUR, lectotype)].

DESCRIPTION.—Thallus greenish gray, thick, continuous, matte. Ascocarps flush with the thallus, lips completely covered by the thalline margin which frequently cracks away from the rest of the thallus, ascocarps occasionally branched, flexuose, 0.5–2.5 mm long. Disc very prominent in surface view, brown and lightly pruinose. Ascocarp transverse section: hymenium 90–100 μm high, epihymenium brown, upper portion of hymenium and all of epihymenium I+ blue. Exciple brown-black, barely closed to barely open, labia quite divergent. Spores 1/ascus, densely muriform, 25–37 \times (80–) 105–130 μm , with broad pale gelatinous outer layer, ca. 15 μm thick, which frequently persists even after ejection from the ascus, I+ blue.

CHEMISTRY.—Norstictic acid, stictic acid, constictic acid.

HABITAT.—On *Cocos* at the shore.

DISCUSSION.—*Graphina collospora* is part of the complex centering around *G. confluens* (Fée) Mueller Argoviensis, which is very similar in morphology and anatomy but lacks the odd colloidal spore layer. It also differs in chemistry (lichexanthone, stictic acid, and constictic acid).

The Dominican specimen seems to represent only the second collection of *G. collospora*.

SPECIMENS EXAMINED.—Ans du Me, sea level, Wirth 520 (US).

42. *Graphina columbina*, new combination

FIGURE 9c; PLATE 8a

Graphis columbina Tuckerman, 1888:123 [type collection: Alabama, USA, Beaumont s.n. (FH, lectotype)].*Fissurina virginalis* Tuckerman ex Nylander, 1889:50 [type collection: Florida, USA, s.n. (US, lectotype)].*Graphis virginalis* Tuckerman ex Eckfeldt, 1890:256.*Graphina virginalis* (Tuckerman ex Nylander) Mueller Argoviensis, 1895b:47.*Phaeographina columbina* (Tuckerman) Zahlbruckner, 1923:436.

DESCRIPTION.—Thallus greenish to brownish, continuous, smooth to matte. Ascocarps fissurine, the margins paler than the surrounding thallus,

straight to flexuose, occasionally branched, 0.5–5 mm long, slender. Disc not visible in surface view. Ascocarp transverse section: hymenium 90–125 μm high, I–; exciple yellowish, rudimentary, labia convergent to somewhat gaping, entire, containing many bark cells. Spores 6–8/ascus, irregularly muriform, 1–3 \times 3–6 locular, clear (!), (8–), 13–19 \times 20–30 (–40) μm , I+ blue.

CHEMISTRY.—Psoromic acid.

HABITAT.—Lowland secondary growth.

DISCUSSION.—The spores of *G. columbina* are clear in all stages, and hence Zahlbruckner's transfer to *Phaeographina* is unnecessary. This species is part of the complex centered around *G. incrustans*. It is most easily distinguished from its relatives by the presence of psoromic acid, a very rare compound in the Graphidaceae.

SPECIMENS EXAMINED.—Roseau Botanic Garden, 100 ft, Wirth 446 (US).

43. *Graphina dimidiata*

FIGURE 9d; PLATE 8b

Graphina dimidiata (Vainio) Zahlbruckner, 1923:404.*Graphis dimidiata* Vainio, 1890:108 [type collection: Brazil, Vainio 322 (TUR, lectotype)].

DESCRIPTION.—Thallus grayish to off-white, continuous to cracked, glossy. Apothecia black, slightly raised, straight to somewhat flexuose, rarely branched, occasionally with a low thalline margin, 0.5–2 (–3) mm long, slender. Disc usually not visible in surface view, occasionally appearing as a lighter line between the labia. Ascocarp transverse section: hymenium 90–115 μm high, epihymenium darkened, I–; exciple open below, lips entire, convergent to spreading, carbonized only on the upper half or less. Spores (?4) 8/ascus, 2–4 \times 4–6 locular, (8–) 10–15 \times (13–) 18–26 μm , I+ blue.

CHEMISTRY.—No substances present.

HABITAT.—Rain forest, mossy forest.

DISCUSSION.—*Graphina dimidiata* is distinct among the small-spored *Graphina* species in its dimidiate, entire exciple, which is carbonized only in the upper portion of the labia.

One of the Dominican specimens (*Hale* 35466) has the thallus irregularly spotted with a bright pink pigment. This coloration is not restricted to the apothecial margins, as in *Phaeographis albida*, and seems to be either an injury or infection.

SPECIMENS EXAMINED.—Madjini, 100 ft, *Hale* 35697 (US); Freshwater Lake, 2600–2800 ft, *Hale* 35466 (US).

44. *Graphina dispersa*

FIGURE 9e; PLATE 8c

Graphina dispersa Redinger, 1933:67 [type collection: Brasil, *Malme* 2038B (S, lectotype)].

DESCRIPTION.—Thallus in the type epilithic and scattered, in the Dominican specimen corticolous, continuous, pale tan, matte. Ascocarps raised, in the type mostly whitish laterally, in the Dominican specimen whitish to concolorous with the thallus, in the type mostly 1 mm long, in the Dominican specimen 1–3 mm long, both rarely branched, straight to slightly curved, both frequently pale to reddish tan above. Disc not visible in surface view. Ascocarp transverse section: hymenium 70–100 μm high in type, 130–150 μm in the Dominican specimen, I–; exciple pale red-brown, closed, labia convergent, internally striate. Spores 6–8/ascus, muriform, 9–12 \times 20–30 μm , I+ blue.

CHEMISTRY.—Norstictic acid.

HABITAT.—Virgin upland rain forest (Dominica only).

DISCUSSION.—The illustration of the exciple that accompanies Redinger's original description is incorrect, in that the exciple is shown as quite dark. Thin sections are difficult to prepare from specimens on rock; presumably the illustration was taken from a rather thick section. The Dominican material differs from the type in being corticolous and more vigorous overall.

Graphina dispersa is similar to *G. chlorocarpa* but differs in spore number and size and in chemistry. Also similar is *Graphina carneoviridis*, which differs in having smaller spores, a paler more poorly developed exciple, and a different chemistry.

SPECIMEN EXAMINED.—Morne Diablotin, 2200–2600 ft, *Hale* 38090 (US).

45. *Graphina frumentaria*

FIGURE 9f; PLATE 8d

Graphina frumentaria (Fée) Mueller Argoviensis, 1880:40.

Graphis frumentaria Fée 1824:45 [type collection: Peru, *Mutis* s.n. (G, lectotype)].

DESCRIPTION.—Thallus buff-gray, smooth to somewhat rugose, glossy, occasionally cracked. Ascocarps

very large and emergent, covered to the apices by the thalline margin, usually unbranched, straight to somewhat curved, 1–4 mm long, to nearly 1 mm wide. Ascocarp transverse section: hymenium 250–300 μm high, I–; exciple yellow, occasionally red-brown below, open, labia convergent, more or less intact, covered completely by pale thalline tissue. Spores 6–8/ascus, densely muriform, 18–24 \times 42–60 μm , I+ blue.

CHEMISTRY.—No substances present.

HABITAT.—Virgin rain forest.

DISCUSSION.—*Graphina frumentaria* is somewhat similar to *G. chlorocarpa* but differs in its very large ascocarps, entire labia, and in having 6–8 spores per ascus. The description and illustration of this species in Redinger (1933:69) are probably incorrect in that the specimen has labia with internal striae and the overall size is distinctly less than the type.

SPECIMEN EXAMINED.—Can-Dom logging area, Newfoundland, 800 ft, *Hale* 35242 (US).

46. *Graphina illinata*, new combination

FIGURE 9g; PLATE 8e

Graphis illinata Eschweiler in Martius, 1833:82 [type collection: Brazil, s.n. (M, lectotype)].

DESCRIPTION.—Thallus slate gray to whitish, smooth, glossy, thick. Ascocarps very protuberant, straight to occasionally flexuose, usually unbranched, covered completely by the thalline margin, only rarely showing a trace of the black exciple, 0.5–6 mm long, mostly ca. 1 mm wide. Disc not visible in surface view. Ascocarp transverse section: hymenium 350–710 (!) μm high, I–; exciple black, massively closed, labia more or less convergent, more or less entire, completely covered by the thalline margin. Spores 1/ascus, densely muriform, 30–50 \times 110–225 μm , I+ blue.

CHEMISTRY.—No substances present (trace norstictic acid on one specimen).

HABITAT.—Virgin upland rain forest.

DISCUSSION.—The traditional concept of *G. illinata*, i.e., as an earlier name for *Graphis anguilliformis*, is quite incorrect. The lectotype has one very large muriform spore per ascus and thus must be transferred to *Graphina*. It is interesting to note that this very large, very distinct and obvious species was found in Dominica by only one of the four

collectors. The implication, of course, is that many other less conspicuous canopy species remain uncollected on the island.

SPECIMENS EXAMINED.—Can-Dom logging area, Brantridge Estate, 1700 ft, *Hale* 35276, 35281, 35284 (US); Can-Dom logging area, Pont Cassé, 2000 ft, *Hale* 35082, 35083, 35124 (US).

47. *Graphina incrustans*

FIGURE 9h; PLATE 8f

Graphina incrustans (Fée) Mueller Argoviensis 1887:47.
Fissurina incrustans Fée, 1824:60 [type collection: South America, s.n. (G, lectotype)].
Graphis rubiginosa Fée, 1824:47 [type collection: South America, s.n. (G, lectotype)].
Graphina rubiginosa (Fée) Mueller Argoviensis, 1887:44.
Graphis glaucoderma Nylander ex Tuckerman, 1888:124 (type collection: Cuba, Wright 61 (FH, lectotype)].
Graphis dehiscens Vainio, 1890:111 [type collection: Brazil, Vainio 306 (TUR, lectotype)].
Fissurina nitidescens Nylander, 1890:108 [type collection: Florida, USA, Calkins 31 (H, lectotype)].
Graphina glaucoderma (Nylander ex Tuckerman) Mueller Argoviensis 1895b:47.
Graphis nitidescens (Nylander) Vainio, 1915:151.
Graphina nitidescens (Nylander) Riddle, 1918:115.
Graphina dehiscens (Vainio) Redinger, 1933:13.

DESCRIPTION.—Thallus yellow-brown to yellow-green, glossy to somewhat matte, smooth, thick, upper layer distinctly prosoplectenchymatous in transverse section. Ascocarps fissurine, starting as a crack flush with the thallus, finally gaping, occasionally branched, usually concolorous with the thallus, nearly round to quite elongate and flexuose, 0.5–6 mm long. Disc exposed but too sunken to be easily visible in surface view. Ascocarp transverse section: hymenium (45–) 75–150 μm high, I–, epihymenium slightly darkened; exciple rudimentary, yellow to pale red-brown, more or less open, labia quite convergent to quite spreading, apices of lips sometimes slightly darkened, with much included bark. Spores 8/ascus, 1–2 (–3) \times 4–6 locular, 6–11 \times 13–35 μm , I– or I+ slow, reddish.

CHEMISTRY.—No substances present.

HABITAT.—Rain forest and elfin forest.

DISCUSSION.—*Graphina incrustans* is a member of a species complex which appears to parallel the fissurine *Graphis* species (see *Graphis triticea*). It is a sporomorph of *Graphis dumastii*; undoubtedly a whole series of sporomorphs will be found between these two groups.

The species listed in synonymy overlap with each other completely and cannot be maintained on any reasonable grounds. We have concentrated on Neotropical species, but many Paleotropic types will undoubtedly be involved here also; we have not yet seen TLC analyses for these.

Most similar to *G. incrustans* is probably *G. babingtonii* (Montagne) Zahlbruckner; this species is tentatively separable by its more strongly gaping ascocarps and in having only 4–6 spores per ascus. *Graphina insculpta* is morphologically identical, separable only in having one very large spore per ascus.

SPECIMENS EXAMINED.—Micotrin, 3000 ft, Wirth 465 (US); South Chiltern Estate, 1200–1500 ft, *Imshaug* 32802 (MSC); Freshwater Lake, 2600–2877 ft, *Imshaug* 32857A (MSC).

48. *Graphina insculpta*

FIGURE 10a; PLATE 9a

Graphina insculpta (Eschweiler in Martius) Mueller Argoviensis, 1888b:507.
Diorygma insculpta Eschweiler in Martius, 1828:9 [type collection: Brazil, s.n. (M, lectotype)].
Graphis insculpta (Eschweiler in Martius) Nylander, 1863:371.

DESCRIPTION.—Thallus greenish to yellow-brown, smooth, glossy, thick, quite prosoplectenchymatous in section. Ascocarps fissurine, concolorous with the thallus, usually unbranched, straight to slightly curved, 0.5–1.5 mm long. Ascocarp transverse section: hymenium 90–120 μm high, I–; exciple rudimentary, yellow to pale red-brown, open, labia convergent to spreading, with much included bark. Spores 1/ascus, densely muriform, 20–30 \times (50–) 70–75 (–100) μm , I– or I+ slow, reddish.

CHEMISTRY.—No substances present.

HABITAT.—Rain forest.

DISCUSSION.—*Graphina insculpta* is morphologically identical to *G. incrustans* and can be separated only by having one very large spore per ascus.

SPECIMENS EXAMINED.—Near Pont Cassé, 1400 ft, *Hale* 37819 (US).

49. *Graphina macella*

FIGURE 10b; PLATE 9b

Graphina macella (Krempelhuber) Mueller Argoviensis, 1880:39.

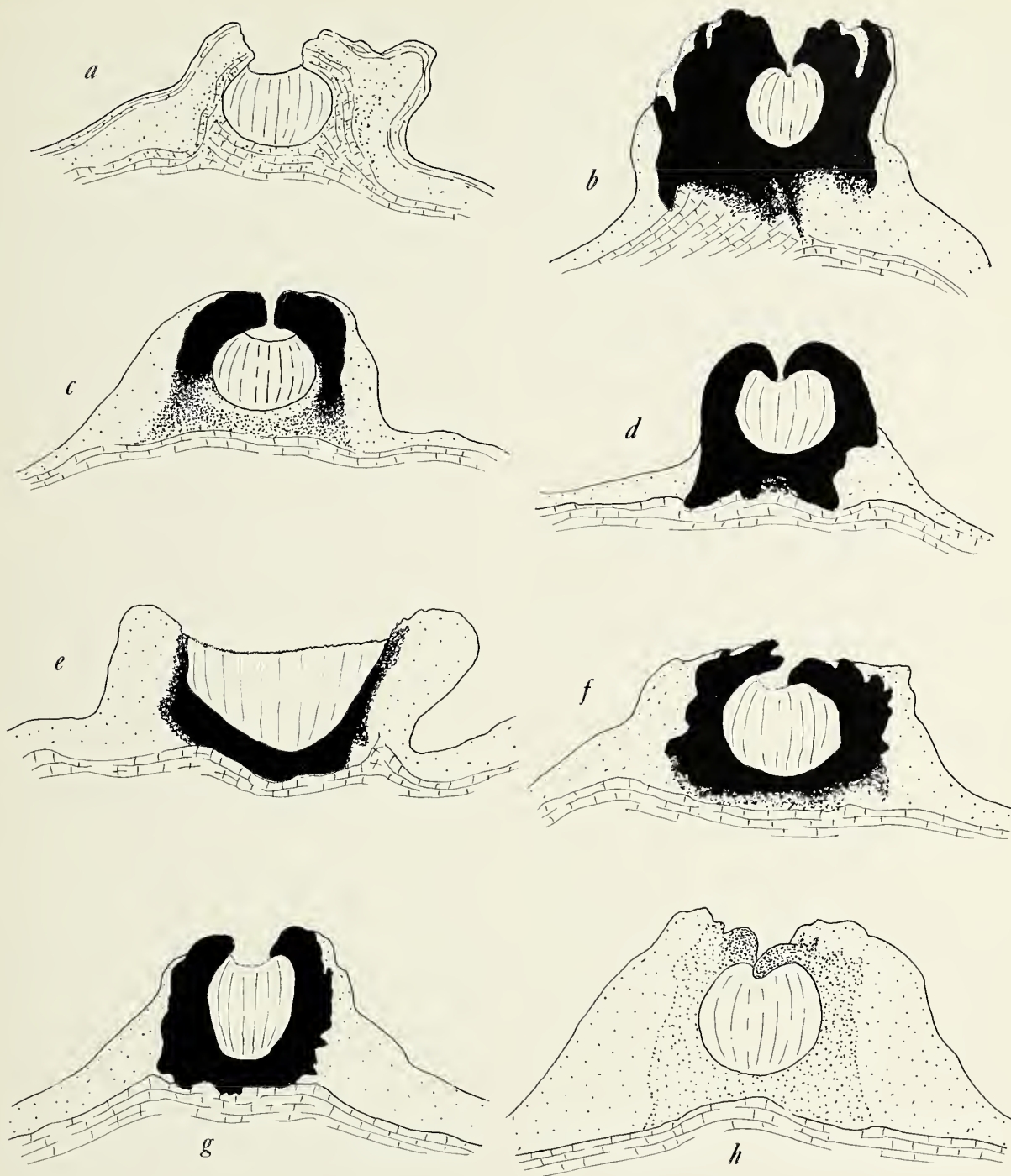


FIGURE 10.—Cross sections of apothecia of *Graphina*: a, *G. insculpta* (lectotype in G); b, *G. macella* (Glaziou 6289B); c, *G. marcescens* (lectotype in G); d, *G. nuda* (Hale 35119); e, *G. platyleuca* (Thiebaut s.n.); f, *G. plurispora* (Malme 998); g, *G. pseudoanaloga* (Duss 1590); h, *G. rufopallida* (Duss 527).

Graphis macella Krempelhuber, 1876:380 [type collection: Brazil, *Glaziou* 6289b (M, lectotype)].

DESCRIPTION.—Thallus gray to white, continuous, smooth to lightly rugose, glossy to somewhat matte. Ascocarps raised but not prominently so, straight to curved, usually unbranched, apically black or black with thin white thalline stripes, laterally covered by the thalline margin, 1–5 mm long, less than 0.5 mm wide. Disc not visible in surface view. Ascocarp transverse section: hymenium 140–160 μm high, I–; exciple black laterally and above, frequently brown or irregularly carbonized below, closed to nearly open, labia convergent, striate. Spores 1/ascus, densely muriform, (20–) 25–40 \times (–65) 95–130 μm , I+ blue.

CHEMISTRY.—No substances present.

HABITAT.—Rain forest (Dominica).

DISCUSSION.—*Graphina macella* is similar to *G. acharii* but is smaller overall, more sunken, consistently has monosporous asci, and has an irregularly carbonized excipular base. In addition to the Brazilian and Dominican material, we have seen specimens from Mexico, indicating that this species will probably be found throughout the Neotropics.

SPECIMEN EXAMINED.—Valley of Desolation, 2800 ft, *Hale* 35723 (US).

50. *Graphina marcescens*

FIGURE 10c; PLATE 9c

Graphina marcescens (Fée) Mueller Argoviensis, 1887:42.

Graphis marcescens Fée 1824:38 [type collection: South America, *Humboldt et Bonpland* s.n. (G, lectotype)].

Graphis intricata Eschweiler in Martius, 1833:79 (non *Graphis intricata* Fée, 1824:42) [type collection: Brazil, *Martius* s.n. (M, lectotype)].

Graphina intricata (Eschweiler in Martius) Mueller Argoviensis, 1888b:510.

Graphina plittii Zahlbruckner, 1928:60 [type collection: Florida, USA, *Plitt* s.n. (US, lectotype; L, isotype)].

DESCRIPTION.—Thallus off-white, continuous, matte to nearly powdery. Ascocarps more or less emergent, rarely branched, quite flexuose, completely covered by a concolorous thalline margin which is easily dislodged, exposing the black exciples below, 1–6 mm long, ca. 0.3 mm wide. Ascocarp transverse section: hymenium (60–) 75–120 (–140) μm , high, I–; exciple black above, more or less closed below by paler yellow to red or brown

tissue, labia convergent, entire to slightly crenate, completely thalline covered. Spores 8/ascus, 1–2 \times 4–5 locular, 5–8 \times 12–16 μm , I+ blue.

CHEMISTRY.—Salazinic acid.

HABITAT.—Upland rain forest (Dominica; see remarks).

DISCUSSION.—*Graphina marcescens* is unlikely to be confused with any other *Graphina* species. Three characteristics account for this individuality: The red-brown exciple base, the presence of salazinic acid, very rare in the family, and the powdery thalline covering, easily rubbed, completely covering the ascocarps. Externally, *G. marcescens* is identical to *Graphis candidissima* Zahlbruckner (1923) but is easily separable from that species by spores and chemistry.

It seems likely that this species will be found to have a wide range, both geographically and ecologically. The Dominican specimen (and probably the type of *G. marcescens*) is from high virgin rain forest; the type of *G. plittii* is from Florida, and hence probably lowland forest. In addition, we have seen a specimen from 2200 meters, collected in India (*Hale* 35312A), which differs from the Neotropical material only in being somewhat larger and in having the exciple base a bit more carbonized.

SPECIMEN EXAMINED.—Can-Dom logging area, Dleau Gommier, 1600–1700 ft, *Hale* 34312A (US).

51. *Graphina nuda*

FIGURE 10d; PLATE 9d

Graphina nuda Magnusson, 1955:266 [type collection: Mauna Kea, Hawaii, *Faurie* 1025b (UPS, holotype)].

DESCRIPTION.—Thallus gray to tan-gray, continuous, smooth to minutely roughened. Ascocarps very prominent, black, straight to slightly curved, unbranched, without a thalline margin, resembling *Graphis adpressa*, 1–2 mm long, slender. Disc not visible in surface view. Ascocarp transverse section: hymenium 135–150 μm high, I–; exciple black usually closed but occasionally irregular at the base, lips intact, convergent. Spores 8/ascus, uniseriate, 1–4 \times 4 locular, 16–18 \times 20–30 μm , I+ blue.

CHEMISTRY.—No substances present.

HABITAT.—Coastal *Cocos* to virgin upland rain forest; apparently of wide ecological amplitude.

DISCUSSION.—*Graphina nuda* is distinctive among

Dominican *Graphina* species in its short, *Opegrapha*-like ascocarps, externally (and internally) indistinguishable from *Graphis adpressa*. Closely related to *G. nuda* is *G. substriatula* (Nylander) Zahlbruckner (1923), which has larger spores and is striate in some portions of the type. Also similar is *G. sulcatula* Mueller Argoviensis (1888d), which has longer, sinuous ascocarps, and exciples that are nearly open and nearly crenate. *Graphina ruiziana* (Fée) Mueller Argoviensis (1887), which is externally and internally very similar, differs in having much smaller spores.

SPECIMENS EXAMINED.—Prince Rupert Bay, Imshaug 33536A (MSC); Can-Dom logging area, Pont Cassé, 2000 ft, Hale 35092, 35119 (US).

52. *Graphina platyleuca*

FIGURE 10c; PLATE 9e

Graphina platyleuca (Nylander) Zahlbruckner, 1923:420.

Graphis platyleuca Nylander, 1868:114 [type collection: New Caledonia, Thiebaut s.n. (H, lectotype)].

Graphina platycarpa Fink, 1927:219 (non *G. platycarpa* (Eschweiler in Martius) Zahlbruckner, 1902:385) [type collection: Puerto Rico, Fink 1774 (MICH, lectotype)].

Graphina platycarpina Zahlbruckner, 1932:214 (nomen novum for *G. platycarpa* Fink).

DESCRIPTION.—Thallus greenish white, continuous or occasionally cracked, matte to nearly powdery-mealy. Ascocarps usually strongly raised, rotund to somewhat elongate, rarely branched, labia completely covered by the thalline margin, 1–2 (–5) mm long, ca. 1 mm wide. Disc prominent, concolorous to brownish black, lightly pruinose. Ascocarp transverse section: hymenium 150–250 μm , high, I+ blue, epihymenium dark; exciple irregularly carbonized, quite black in parts, red-brown in other patches, closed, lips quite divergent, entire. Spores 1/ascus, densely muriform, 35–40 \times 120–165 μm , I+ blue.

CHEMISTRY.—Protocetraric acid only (types of *G. platyleuca*, *G. platycarpa*), or protocetraric acid with salazinic acid and norstictic acid (see discussion).

HABITAT.—Primary rain forest (Dominica).

DISCUSSION.—As presently recognized, *G. platyleuca* is a chemically heterogeneous species. However, protocetraric acid is quite rare in the Graphidaceae and serves to tie the Dominican specimen into the taxon. The only other material we have

seen that is referable here is the “type” of one of Nylander’s *nomina nuda*, *Graphis glaucoleuca*, from Cuba. This specimen is chemically like the Dominican material. Additional collections may reveal that *G. platyleuca* shows similar chemical variation to that found in *Phaeographis exaltata*.

Most similar to *G. platyleuca* is *G. confluens* (Fée) Mueller Argoviensis (1887); the latter species can be distinguished by somewhat less emergent ascocarps and a different chemistry (lichexanthone, stictic acid, and constictic acid).

SPECIMEN EXAMINED.—Dleau Gommier Forest Reserve, 1200 ft, Hale 37955 (US).

53. *Graphina plurispora*, new combination

FIGURE 10f; PLATE 9f

Graphina pseudosophistica var. *plurispora* Redinger, 1933:36 [type Collection: Brasil, Malme 998 (S, lectotype)].

DESCRIPTION.—Thallus continuous, gray-white, smooth and glossy to matte (on the same thallus). Ascocarps barely raised, black above, frequently with white stripes, with a well-developed thalline margin laterally, quite flexuose, 2–5 mm long, slender. Disc not visible in surface view. Ascocarp transverse section; hymenium 60–100 μm high (on the same specimen), I–; exciple very variable (within one ascocarp), black, distinctly open to distinctly closed, lips convergent, perfectly intact to quite striate. Spores beginning as 8/ascus, but only (2–) 4–6 maturing, muriform, 1–3 \times 8–13 locular, 10–15 \times (27–) 35–50 (–60) μm , I+ blue.

CHEMISTRY.—No substances present.

HABITAT.—Cultivated areas above 1500 feet (Dominica only).

DISCUSSION.—Redinger’s variety differs from the type of *Graphina pseudosophistica* in two important respects. The latter has consistently monosporous asci and has the “quintaria” unknowns. Because of these differences, we have raised the variety to species rank. Still, *Graphina plurispora* is both highly variable and part of a very confusing array of species. Most closely related are the following

Graphina disserpens (Nylander) Mueller Argoviensis (1880) is tentatively separable because of the quite dendritically branched ascocarps and consistently open exciples.

Graphina elongatoradians Fink (1927) is another

dendritically branched relative with longer, more slender ascocarps, with open exciples, and a different chemistry (two unknown substances).

Graphina subvelata (Stirton) Zahlbruckner (1923) differs in being non-striate and in having open exciples. See Hayward (1978) for a discussion of *G. subvelata* and its near relatives, including New World species.

In addition, *G. plurispora* bears a number of similarities to the *G. antillarum* complex; for a more complete discussion, see the latter species.

SPECIMENS EXAMINED.—South Chiltern Estate Road, 1500–1700 ft, *Imshaug* 32724A, 32727 (MSC).

54. *Graphina pseudoanaloga*

FIGURE 10g; PLATE 10a

Graphina pseudoanaloga (Vainio) Zahlbruckner, 1923:421.
Graphis pseudoanaloga Vainio, 1915:145 [type collection: Guadeloupe, *Duss* 1590 (TUR, lectotype)].

DESCRIPTION.—Thallus gray-white, thin, continuous, matte. Ascocarps slightly raised, black above, straight to flexuose, rarely branched, covered about half-way by the thalline margin, 0.5–4 mm long, slender. Disc not visible in surface view. Ascocarp transverse section: hymenium 75–115 μm high, interspersed (apparently clear in *Wirth* 526), epihymenium dark, I–; exciple black, closed to occasionally nearly open, labia convergent, entire to barely crenate, rarely with an occasional stria (all on one thallus). Spores 8/ascus, 1–3 \times 7–10 locular, 9–12 \times 22–45 μm , I+ blue.

CHEMISTRY.—Norstictic acid.

HABITAT.—Beach to upland virgin rain forest; apparently of wide ecological amplitude.

DISCUSSION.—*Graphina pseudoanaloga* is very similar to *G. analoga* (Nylander) Zahlbruckner (1923), which differs in having smaller spores and an open exciple.

SPECIMENS EXAMINED.—Cabrit, sea level, *Wirth* 526 (US); Can-Dom logging area, Brantridge Estate, 1700 ft, *Hale* 35283 (US).

55. *Graphina rufopallida*

FIGURE 10h; PLATE 10b

Graphina rufopallida (Vainio) Zahlbruckner, 1923:423 (“*rufopallens*,” *sphalm.*).
Graphis rufopallida Vainio, 1915:149 [type collection: Guade-

loupe, *Duss* 527 (TUR, lectotype)].

Graphis vermicularis Vainio, 1915:148 [type collection: Shawford Estate, Dominica, *Elliott* 1852 (TUR, lectotype)].

Graphina vermicularis (Vainio) Zahlbruckner, 1923:430.

DESCRIPTION.—Thallus off-white, smooth, continuous. Ascocarps somewhat emergent, tan to red-brown, rarely branched, flexuose and intertwined, 1–7 mm long, slender. Disc not visible in surface view. Ascocarp transverse section: hymenium 70–100 μm high, I–; exciple more or less open, labia convergent, more or less striate, dark red-brown or fuscous apically (but not carbonized), paler yellow-brown below. Spores 6–8/immature ascus, apparently always aborting to 2–4/mature ascus, densely muriform, 15–30 \times 36–75 μm , I+ blue.

CHEMISTRY.—No substances present.

HABITAT.—Upland rain forest.

DISCUSSION.—*Graphina rufopallida* is most similar to *G. balbisii* (see discussion under *G. chlorocarpa*), from which it differs in the lower, much longer, more slender and intricating ascocarps.

We have seen no specimens of this species other than the two types cited.

SPECIMEN EXAMINED.—Shawford Estate, *Elliott* 1852 (TUR).

56. *Graphina suberythrella*, new species

FIGURE 11a; PLATE 10c

DESCRIPTION.—Thallus continuous, laevis, stratum corticale bene evolutum. Apothecia subimmersa, flexuosa, vulgo simplicia, 2–4 mm longa, disco lato, pruinoso. Excipulum integrum, flavidum vel rufoferrugineum, labiis integris, divergentibus. Hymenium 110–140 μm altum, I+ coeruleum. Asci 8 spori; sporae decolores, murales, loculis horizontalibus 5–7, loculis transversis 1–3, 10–14 \times 17–28 μm , I+ coeruleae, in juventute halonae indutae.

Thallus gray, glossy, continuous, rather thick, cortical layer compact and distinct. Ascocarps barely raised, flexuose, occasionally branched, 2–4 mm long, slender, concolorous with the thallus. Disc broad, dark gray, lightly pruinose. Ascocarp transverse section: hymenium 110–140 μm high, at least the epihymenium I+ blue; exciple yellow to red-brown, closed, lips intact and divergent. Spores 8/ascus, 1–3 \times 5–7 locular, halonate in early stages, 10–14 \times 17–28 μm , I+ blue.

CHEMISTRY.—Norstictic acid.

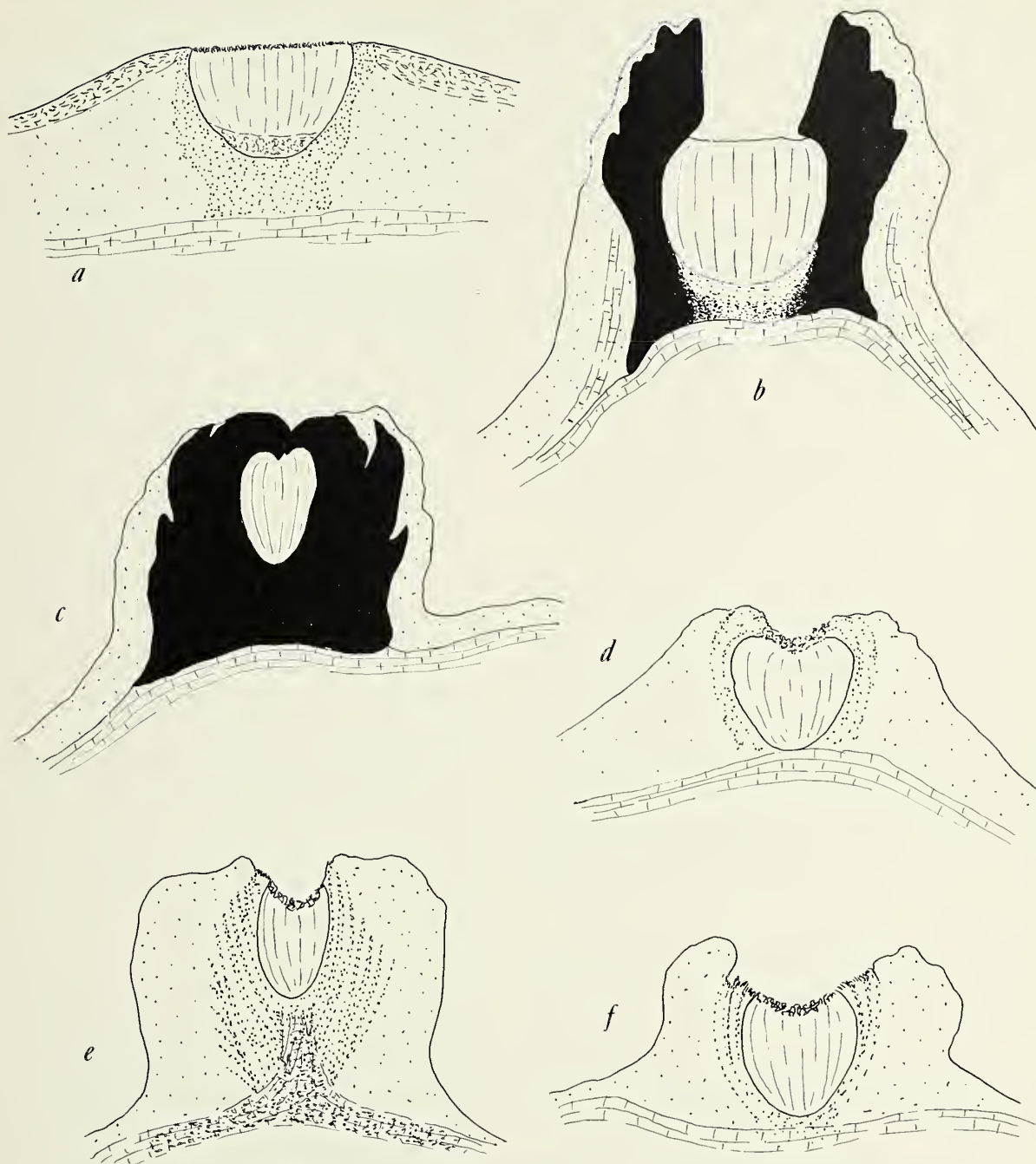


FIGURE 11.—Cross sections of apothecia of *Graphina*: a, *G. suberythrella* (Imshaug 32699); b, *G. triphoroides* (Hale 35161); c, *G. vestitoides* (Fink 1986); d, *G. virginea* (Wirth 547); e, *G. virginea* (lectotype of *G. triangularis*, Pringle 17); f, *G. virginea* (lectotype of *G. obtectula*, Tonduz).

HOLOTYPE.—Cultivated area, South Chiltern Estate Road, Dominica, elevation 1500–1700 feet, Imshaug 32699 (MSC); isotype, US).

DISCUSSION.—*Graphina suberythrella* resembles

G. erythrella (Montagne) Zahlbruckner (1923), but differs in its more immersed ascocarps, gray disc, I–hymenium and larger spores. Also similar is *G. insignis* (Vainio) Zahlbruckner (1923), which dif-

fers in having wider ascocarps and smaller spores, and in lacking both norstictic acid and the I+ hymenium.

SPECIMEN EXAMINED.—Can-Dom logging area, Newfoundland, 800 ft, *Hale* 35224 (US).

57. *Graphina triphoroides*, new species

FIGURE 11b; PLATE 10d

DESCRIPTION.—Thallus continuus, farinosus. Apothecia alte sessilia, simplicia, margine thallino usque ad verticem vestita, 1–6 mm longa, 1 mm lata. Excipulum dimidiatum, fuliginum, labiis integris vel irregulariter crenulatis, erectis vel convergentibus; hymenium 250–700 μ m altum, I–; Asci 6 (–8?) spori; sporae decolores, murales, loculis horizontalibus 7–10, loculis transversis 2–4, 18–30 \times 47–75 μ m, I+ coeruleae.

Thallus white to off-white, continuous, mealy. Ascocarps large, very protuberant, unbranched, covered to the apices by a mealy concolorous thalline margin, irregularly blackened where the covering is rubbed, 1–6 mm long, 1 mm wide. Disc usually not visible in surface view. Ascocarp transverse section: hymenium 250–700 (!) μ m high, I–; exciple black, more or less yellow-brown and open below, labia erect to convergent, entire to somewhat irregular in outline. Spores 6 (–8?)/ascus, muriform, 2–4 \times 7–10 locular, 18–30 \times 47–75 μ m, I+ blue.

CHEMISTRY.—Stictic acid.

HOLOTYPE.—Can-Dom logging area, Dleau Gommier, 1600–1700 ft, *Hale* 35161, January 1969 (US).

DISCUSSION.—*Graphina triphoroides* is part of a very distinct group of three New World species, all characterized by very large, thalline-covered apothecia and dimidiate, carbonized exciples. *Graphina triphora* (Nylander) Mueller Argoviensis (1880) differs in having 3–4 spores per ascus, no lichen acids, and carbonization restricted more to the upper portions of the labia. *Graphina cleitops* (Fée) Mueller Argoviensis (1887), the third species, differs in being monosporous.

SPECIMENS EXAMINED.—Can-Dom logging area, Dleau Gommier, 1600–1700 ft, *Hale* 35128 (US); *Wright* 15, Cuba (US) ("type" of *Graphis triphoroides* Nylander, unpublished name).

58. *Graphina vestitoides*

FIGURE 11c; PLATE 10e

Graphina vestitoides Fink, 1927:218 [type collection: Puerto Rico, *Fink* 1986 (MICH, lectotype)].

Phaeographis cerviculata Redinger, 1935:76 [type collection: Brazil, *Malme* 3531 (S, lectotype; UPS, isotype)].

DESCRIPTION.—Thallus gray, continuous, smooth. Ascocarps quite protuberant, frequently branched, flexuose, varying from black above and partially covered by a thalline margin to concolorous (completely covered), to 10 mm long, ca. 0.5 mm wide. Ascocarp transverse section: hymenium 150–210 μ m high, I–; exciple black, usually closed, lips convergent, striate to nearly entire. Spores 4–6 (–8)/ascus, biocellate only in the terminal few sections, 12–18 \times 85–140 μ m, I+ blue.

CHEMISTRY.—No substances present.

HABITAT.—Upland virgin and secondary forest.

DISCUSSION.—*Graphina vestitoides* is separable from *G. acharii* only in the peculiarly biocellate spores, which additional collections may prove to be an unreliable character.

The type material of *Phaeographis cerviculata* has mature spores that are quite clear, and the specimen is identical to *G. vestitoides*.

SPECIMENS EXAMINED.—Freshwater Lake, 2600–2877 ft, *Imshaug* 32859A (MSC); near Pont Cassé, 1400 ft, *Wirth* 544a (US).

59. *Graphina virginea*

FIGURE 11d,e,f; PLATE 10f

Graphina virginea (Eschweiler in Martius) Mueller Argoviensis, 1880:41.

Leiogramma virgineum Eschweiler in Martius, 1833:98 [type collection: Brazil, *Martius* s.n. (M, lectotype)].

Graphina obtectula Mueller Argoviensis, 1892b:153 [type collection: Costa Rica, *Pittier* 6166 (G, lectotype); Figure 11f)].

Graphina melaleuca Mueller Argoviensis, 1895c:144 [type collection: Roseau, Dominica, *Eckfeldt* 70 (G, lectotype)].

Graphina palmeri Zahlbruckner, 1921:231 [type collection: Mexico, *Pringle* 9 (MICH, isotype)].

Graphina triangularis Zahlbruckner 1921:232 [type collection: Mexico, *Pringle* 17 (MICH, isotype)].

Graphis collosorella Vainio, 1923:141 [type collection: Trinidad, *Thaxter* 10 (TUR, lectotype)].

Graphina collosorella (Vainio) Zahlbruckner, 1923:212.

DESCRIPTION.—Thallus greenish white to gray, thick, continuous except for a fissure usually paralleling each ascocarp, smooth to mealy, occasion-

ally quite rugose (when ascocarps are densely clustered). Ascocarps nearly flush with the thallus, rarely somewhat raised, margins concolorous to much paler than the thallus, occasionally branched, flexuose, 1–5 mm long, slender. Disc in surface view varying from concealed to quite broad, concolorous to darker than the thallus. Ascocarp transverse section: hymenium 120–200 μm high, epihymenium darkened, at least the epihymenium I+ blue. Exciple yellowish, rudimentary, sometimes thickened below and/or with a basal dark (nearly carbonized) band (see discussion), labia more or less divergent, occasionally with internal striae (see discussion) but otherwise entire. Spores 2–3, 4–6 or 8/ascus (!), most numbers occurring within a single thallus, 1–4 (–7) \times 11–20 locular, (12–) 15–25 \times 50–80 (–130) μm , I+ blue.

CHEMISTRY.—At least one of the 3 so-called “Quintaria” unknowns; trace of stictic acid and constictic acid (type of *G. virginea* only).

HABITAT.—Secondary growth and cultivated trees and shrubs, from sea level to over 1000 meters.

DISCUSSION.—In its usual form *Graphina virginea* is an extremely vigorous species, forming thalli up to 15 cm in diameter. The thallus is normally greenish white, matte, and continuous except for characteristic fissures bordering the ascocarp margin. The ascocarps themselves are commonly slightly paler than the rest of the thallus, and do not occur in close proximity to each other. In all likelihood, the species is weedy and of rapid growth, as large colonies are commonly found on such fast-growing cultivated plants as cacao and blue Mahoe (*Hibiscus*).

Internally, this most common form of the species has a rather rudimentary exciple and a very variable number of spores per ascus.

Morphologically and anatomically, *Graphina collosorella* and *G. obtectula* cannot be separated from the normal form of *G. virginea*.

The other taxa listed as synonyms all show some

structural variation from the typical pattern. In the case of *G. palmeri* and *G. melaleuca* the thallus in surface view appears quite rugose and the ascocarps somewhat emergent. It seems quite likely that this appearance comes with age; dense clustering of more typical ascocarps, with their associated fissures, could easily produce such a form. A probable additional synonym for this “rumpled” variant of *G. virginea* is *G. monophora* (Nylander) Zahlbruckner (1923).

The type of *G. melaleuca* also has a broader, browner disc than is normally found in *G. virginea*; externally this specimen is indistinguishable from *G. mendax* (Nylander) Mueller-Argoviensis (1888a). The different disc is, however, a matter of degree rather than of kind; occasionally one can find such discs on parts of more typical thalli.

Graphina palmeri shows the internal striae that seem to arise with age and lateral compaction of the old hymenium; we do not find such striae to be at all dependable in distinguishing species (see *Graphina colliculosa* for a parallel variation).

The internal striae, coupled with a more or less continuous semicarbonized band below the exciples, is also characteristic of the type of *G. triangularis*, which externally is much like typical *virginea*. The band is occasionally found in thalli of quite normal *G. virginea*, frequently unconnected with the ascocarps. The thickened exciple base of the type of *G. triangularis* is another condition that we feel may well be simply a factor of age (again, see *G. colliculosa* for parallels).

All the forms of *G. virginea* are tied strongly together by their chemistry. All have the rather rare I+ blue reaction of (at least) the epihymenium; all share at least two of the three “Quintaria” acids.

SPECIMENS EXAMINED.—Brookhill Estate, 100–150 ft, *Imshaug* 33321A (MSC); Cocoa Centre on Layou River, 200 ft, *Wirth* 517 (US); north of Pont Cassé, 1400 ft, *Wirth* 543, 545, 547, 548 (US).

Key to the Species of *Phaeographina*

- 1 Exciple with carbonized areas.
 2. Exciples carbonized and closed below63. *P. cf. difformis*
 2. Exciples carbonized only at labial tips.
 3. Ascocarps massive, 1–3 mm wide; no substances present61. *P. caesiopruinosa*
 3. Ascocarps slender, less than 0.4 mm wide; stictic acid present65. *P. oscitans*

1. Exciple uncarbonized.
 4. Labia convergent; spores more than 40 μm long64. *P. elliottii*
 4. Labia divergent, exposing the disc; spores less than 40 μm long.
 5. Ascocarps prominently raised, commonly over 5 mm long; norstictic acid present60. *P. atrovermicularis*
 5. Ascocarps barely raised, less than 5 mm long; norstictic acid absent.
 6. Spores 20–27 μm long; stictic acid present65. *P. oscitans*
 6. Spores 33–35 μm long; no substances present62. *P. coriaria*

60. *Phaeographina atrovermicularis*, new species

FIGURE 12a; PLATE 11a

DESCRIPTION.—Thallus continuus, sublaevigatus. Apothecia adpresso-sessilia, vulgo ramulosa, 3–10 mm longa, disco dilatato, nigro. Excipulum dimidiatum, fuscum, labiis integris, divergentibus; hymenium 145–220 μm altum, I–. Asci 6–8 spori; sporae fuscescentes, murales, loculis horizontalibus 6–9, loculis transversis 1–4, 15–17 \times 25–35 μm , I+ coeruleae.

Thallus thin, light tan, continuous to apparently eroded except near the ascocarps, smooth to matte. Ascocarps very long, raised, frequently branched, the pale thalline margin very prominent, 3–10 mm long, slender. Disc very prominent, black, occasionally faintly pruinose. Ascocarp transverse section: hymenium 145–220 μm high, I–, lightly beaded-inspersed; exciple open below, laterally brownish-black, labia divergent, intact, bounded by a thick parenchymatous thalline margin. Spores 6–8/ascus, 1–4 \times 6–9 loculed, 15–17 \times 25–35 μm , I+ blue.

CHEMISTRY.—Norstictic acid.

HOLOTYPE.—Can-Dom logging area, Brantridge Estate, Dominica, elevation 1700 feet, *Hale* 35278 (US).

DISCUSSION.—By virtue of its long black ascocarps, *Phaeographina atrovermicularis* is quite distinct and is apparently not closely related to any other New World species. Most similar is *P. intercedens* Mueller Argoviensis (1888e), which differs in having shorter, broader, stockier ascocarps, larger spores, an unknown acid in addition to norstictic, and no trace of carbonization in the exciple. Also somewhat similar is the widespread *P. caesiopruinosa*, which has much shorter, broader ascocarps, strongly pruinose discs, and lacks norstictic acid.

SPECIMENS EXAMINED.—Can-Dom logging area, Pont Cassé, 2000 ft, *Hale* 35093 (US); rain forest, Jean Estate, 2000 ft, *Hale* 35068 (US).

61. *Phaeographina caesiopruinosa*

FIGURE 12b; PLATE 11b

Phaeographina caesiopruinosa (Fée) Mueller Argoviensis, 1887:49.

Arthonia caesiopruinosa Fée, 1837:36 [type collection: South America, s.n. (G, lectotype)].

DESCRIPTION.—Thallus pale brown, smooth to slightly roughened, continuous. Ascocarps quite elevated, rarely branched, straight to flexuose, thalline margin reaching to disc, 1–10 mm long, 1–3 mm wide. Disc very prominent in surface view, lightly to very heavily pruinose. Ascocarp transverse section: hymenium 150–200 μm high, I–, epihymenium darkened; exciple black laterally, open below, lips divergent. Spores (4–) 6–8/ascus, densely muriform, 12–17 \times 45–75 (–100) μm , I+ slow, reddish blue.

CHEMISTRY.—No substances present.

HABITAT.—Cultivated areas, uplands.

DISCUSSION.—*Phaeographina caesiopruinosa* is a very common New World species, unlikely to be misidentified. All other New World species with very large ascocarps and carbonized exciples have monosporous asci.

SPECIMEN EXAMINED.—South Chiltern Estate, 1500–1700 ft, *Imshaug* 32731 (MSC).

62. *Phaeographina coriaria*, new species

FIGURE 12c; PLATE 11c

DESCRIPTION.—Thallus continuus, laevis, coriaceus. Apothecia adpresso-sessilia, recta vel arcuata, simplicia vel raro ramulosa, 1–5 mm longa et ca. 0.3 mm lata, disco dilatato, nigro, leviter pruinoso. Excipulum rufo-ferrugineum, dimidiatum, labiis integris, divergentibus; hymenium ca. 150 μm altum, I–. Asci 4–6 (–8?) spori; sporae fuscescentes, mu-

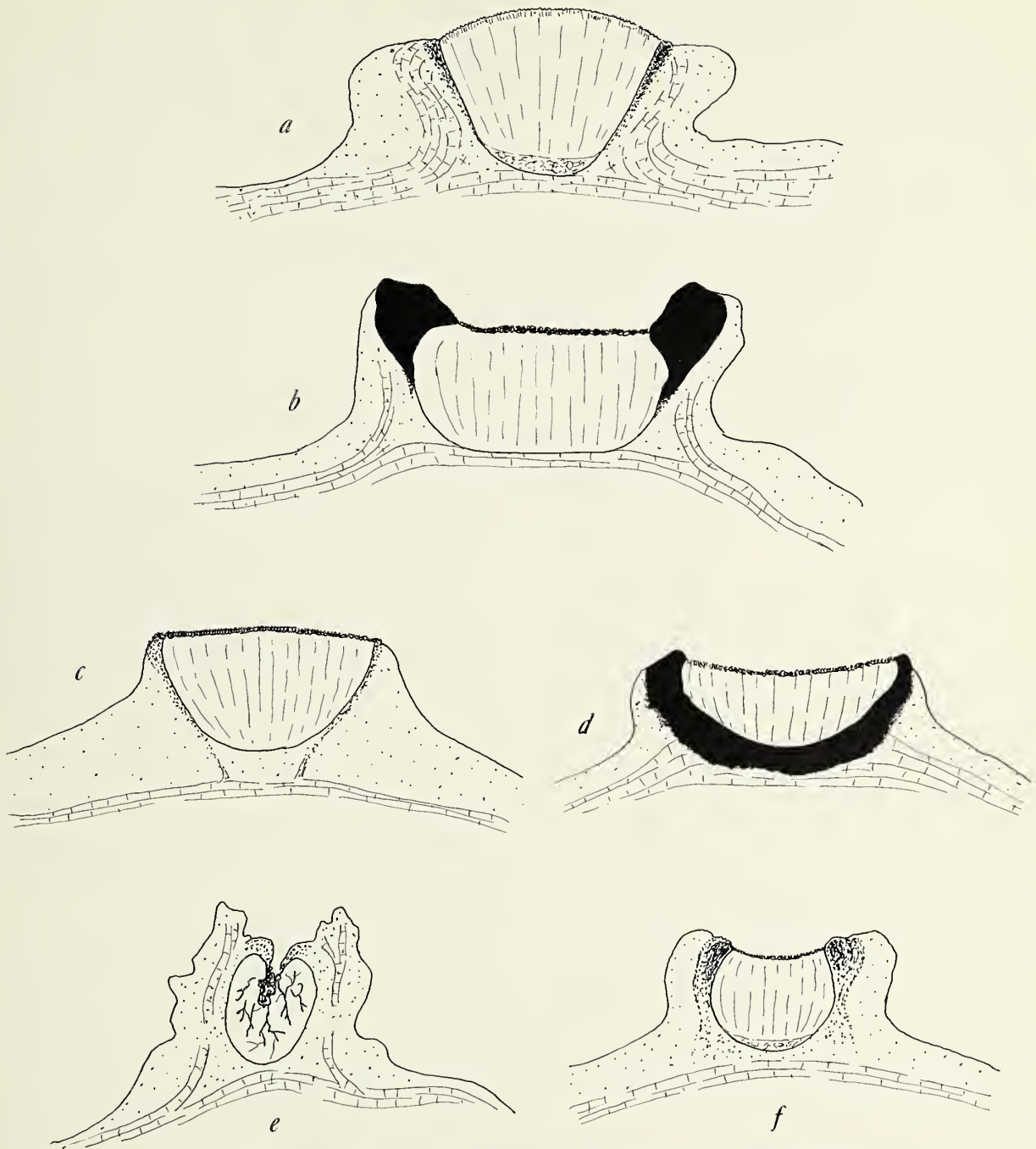


FIGURE 12.—Cross sections of apothecia of *Phaeographina*: a, *P. atrovermicularis* (Hale 35278); b, *P. caesiopruinosa* (lectotype in G); c, *P. coriaria* (Hale 35378); d, *P. difformis* (Fink 1874); e, *P. elliotii* (Elliott 1338); f, *P. oscitans* (Mann s.n.).

rales, loculis horizontalibus 8–10, loculis transversis 1–3, $9\text{--}10 \times 33\text{--}35\ \mu\text{m}$, I+ rufo-fuscae.

Thallus continuous, smooth, tan, resembling velum. Ascocarps slightly raised, straight to some-

what curved, rarely branched, 1–5 mm long, ca. 0.3 mm wide. Disc broad, black, with a light pruina. Ascocarp transverse section: hymenium ca. $150\ \mu\text{m}$ high, beaded, epihymenium dark, I–; exciple

rudimentary to very pale below, laterally red-brown, lips intact, divergent. Spores 4–6 (–8?)/ascus, brown, 8–10 × 1–3 locular, 9–10 × 33–35 μm , I+ red, slowly darkening.

CHEMISTRY.—No substances present.

HOLOTYPE.—Mossy forest, Morne Anglais, Dominica, elevation 3000–3600 feet, *Hale* 35378 (US).

DISCUSSION.—*Phaeographina coriaria* is most similar to the following three New World species:

Phaeographina arechavaletae Mueller Argoviensis (1888c) differs in having distinctly carbonized labia and rotund spores.

Phaeographina caracasana Mueller Argoviensis (1887) differs in having much broader ascocarps with rounder apices and in having smaller spores.

Phaeographina elliptica Wirth and Hale (1963) differs in chemistry and in having monosporous asci.

63. *Phaeographina* cf. *difformis*

FIGURE 12d; PLATE 11d

Phaeographina difformis Fink, 1927:220 [type collection: Aibonito, Puerto Rico, *Fink* 1874 (MICH, lectotype)].

DESCRIPTION.—Thallus thin, continuous, glossy, greenish gray. Ascocarps nearly round to elongate and irregular, ends round, occasionally shortly branched, partly immersed, 0.8–1.5 mm long, ca. 0.8 mm wide, with a raised thalline margin. Disc broad, brown-black, occasionally faintly pruinose. Ascocarp transverse section: hymenium 90–125 μm high, epihymenium very dark, I–; exciple brown-black, closed, lips intact, divergent. Spores 8/ascus in the type, 4/ascus in the Dominican specimen, densely muriform, pale to brown in the type, mostly pale in the Dominican specimen, 10–15 × (25–) 30–48 μm in the type, 18–22 × 55–75 in the Dominican specimen, I+ blue.

CHEMISTRY.—Unknown in the type, no substances present in the Dominican specimen.

HABITAT.—Elfin forest (Dominican specimen only).

DISCUSSION.—Although the Dominican specimen is externally identical to the type, and is indistinguishable in cross-section, the spore size and number make this identification tentative. In addition, it should be noted that both specimens have large

numbers of clear spores, making this species difficult to assign to genus. In fact, this species may represent a link to the smaller members of the *Graphina confluens* alliance, such as *G. cymbographa* (Nylander) Zahlbruckner (1923), which is strikingly similar.

Very similar to *P. difformis* is *P. explicans* Fink ex Hedrick (1933), which differs in its more elongate, rather sunken apothecia.

SPECIMEN EXAMINED.—Summit of Morne Diablotin, 4300–4550 ft, *Imshaug* 32913A (MSC).

64. *Phaeographina elliotii*

FIGURE 12e; PLATE 11e

Phaeographina elliotii (Vainio) Zahlbruckner, 1923:438.
Graphis elliotii Vainio, 1915:143 [type collection: Dominica, Roseau Valley, *Elliott* 1338 (TUR, lectotype)].

DESCRIPTION.—Thallus thin, whitish, matte, continuous. Ascocarps slightly raised, rarely branched, straight to somewhat curved, thalline margin prominent, to 1.5 mm. long, slender. Disc concealed to open and dark gray. Ascocarp transverse section: hymenium completely (?) disintegrated in the type, I+ fide Vainio; exciple yellow-red, not well developed, lips convergent to quite spreading, tips brown, dark portions probably derived (at least in part) by lateral compression of the dark epihymenium. Spores (fide Vainio) 2–8/ascus, muriform, 22–28 × 44–54 μm .

CHEMISTRY.—No substances present.

HABITAT.—“On trees in Roseau Valley.”

DISCUSSION.—The type of *Phaeographina elliotii* now seems to be completely sterile. Both externally and internally, the type specimen closely resembles *Phaeographis albida*; it may be possible that Vainio mistook entire disintegrating asci for spores. We have seen no other material that might be referable to this *Phaeographina* species

65. *Phaeographina oscitans*

FIGURE 12f; PLATE 11f

Phaeographina oscitans (Tuckerman) Zahlbruckner, 1923:442.
Graphis oscitans Tuckerman, 1868:231 [type collection: Oahu, Hawaii, *Mann* s.n. (FH, lectotype)].

DESCRIPTION.—Thallus continuous, smooth to matte, off-white. Ascocarps slightly raised, flexuose, rarely branched, pale thalline margins prominent, 1–2 mm long, slender. Disc prominent, gray-black. Ascocarp transverse section: hymenium 125–150 μm high, I–; exciple rudimentary below, yellow laterally, lips slightly convergent to divergent, more or less carbonized apically, entire to once-sulcate. Spores 8/ascus, brown, $1\text{--}3 \times 6\text{--}8$ locular, $6\text{--}9 \times (15\text{--}) 20\text{--}27 \mu\text{m}$, I+ blue.

CHEMISTRY.—Stictic acid.

HABITAT.—Virgin upland rain forest (Dominica only).

DISCUSSION.—*Phaeographina oscitans* is externally very similar to *Phaeographis albida*, but can easily be separated by spores and chemistry. Also quite similar is *Phaeographina pachnodes* (Fée) Mueller Argoviensis (1887), which differs in having larger spores, no trace of striae, and in having norstictic acid; and *P. turgida* (Fée) Mueller Argoviensis (1887), which would seem to be the TLC negative equivalent of *P. pachnodes*.

SPECIMENS EXAMINED.—Can-Dom logging area, Pont Cassé, 2000 ft, *Hale* 35127, 35131 (US).

Incorrect and Omitted Names

Graphis bonplandiae: See *Graphis triticea* for Elliott 533.

Graphis cooperta: See *Graphis anguilliformis* for Elliott s. n.

Graphis (*Phaeographis*) *diversa*: See *Phaeographis exaltata* for Elliott 526.

Graphis duplicata: See *Graphis rimulosa* for Elliott 125 and *Graphis flexibilis* for Elliott 1954 pro parte.

Graphis duplicata var. *subduplicata* Vainio: Elliott 1509 is sterile.

Graphis lactea: Elliott 535 is the type of *G. lactea* var. *dominicana* Vainio; see *Graphis tachygrapha*.

Graphis lactea var. *clausa*: See *Graphis insidiosa* for Elliott 1511.

Graphis lineola: See *Graphis leptocarpa* for Elliott 1535.

Graphis (*Phaeographis*) *lobata*: The only Dominican collection (Elliott 1365 in TUR) is correctly identified to species, but it is not included in our list because the generic status is unclear. It is probably closer to *Phaeotrema* in the Thelotremaaceae.

Graphis (*Phaeographis*) *medusaeformis*: Elliott 529 in BM is a fragmentary specimen, which may be an immature *Phaeographis exaltata*. There is no specimen so identified in TUR.

Graphis (*Graphina*) *subnitida*: Elliott 171 is indeterminable.

Graphis tenella var. *epiphaea* Vainio: Not found in TUR or BM and presumed to be lost or misfiled.

Graphis (*Graphina*) *vermicularis*: See *Graphina rufopallida* for Elliott 1852.

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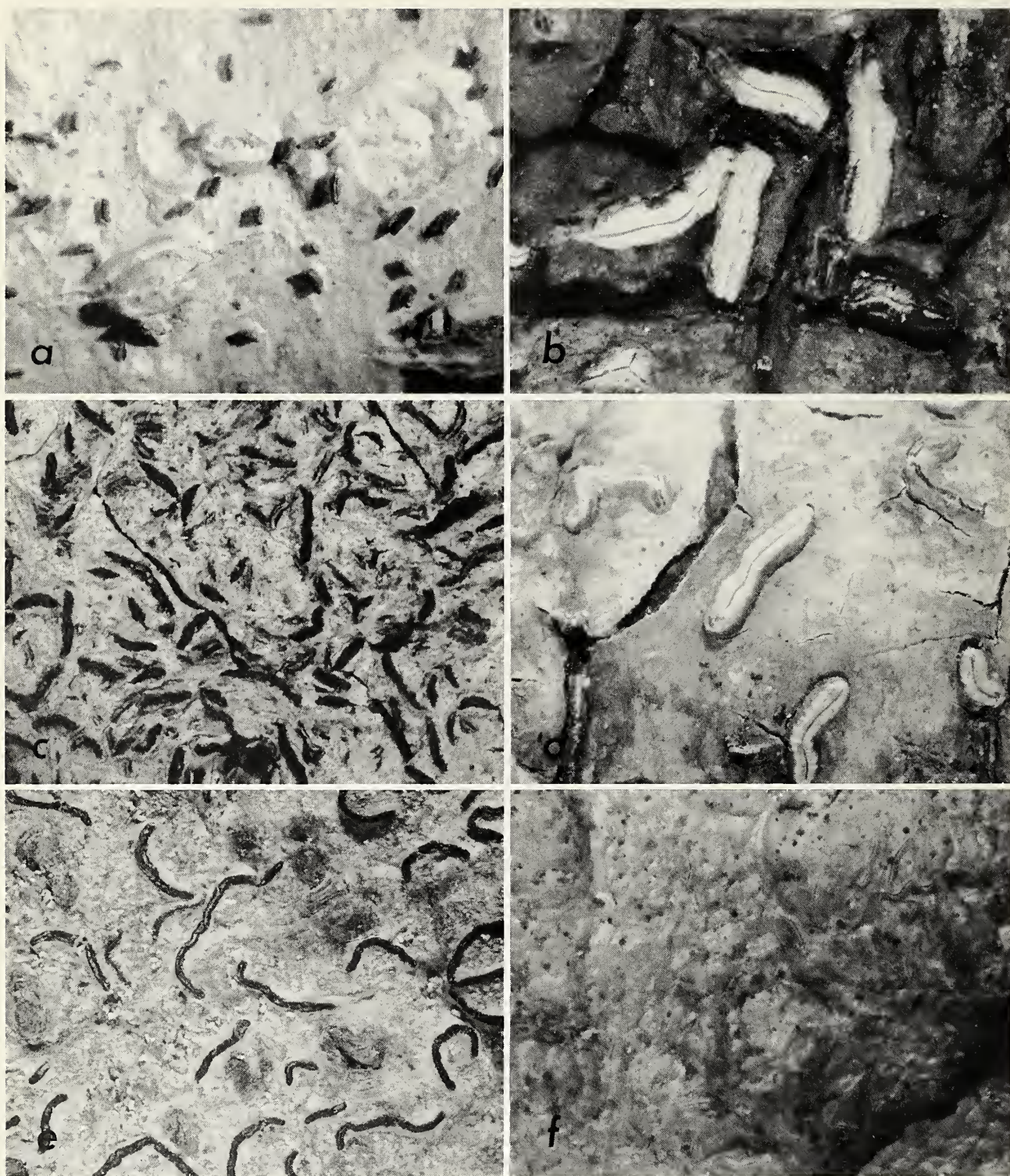


PLATE 1.—Species of *Graphis*: a, *G. adpressa* (Hale 35487); b, *G. afzelii* (Imshaug 33489A); c, *G. anfractuosa* (Wirth 538); d, *G. anguilliformis* (Hale 35282); e, *G. desquamescens* (Hale 35449); f, *G. dumastioides* (Hale 37722). (Plates 1–10 $\times 10$.)

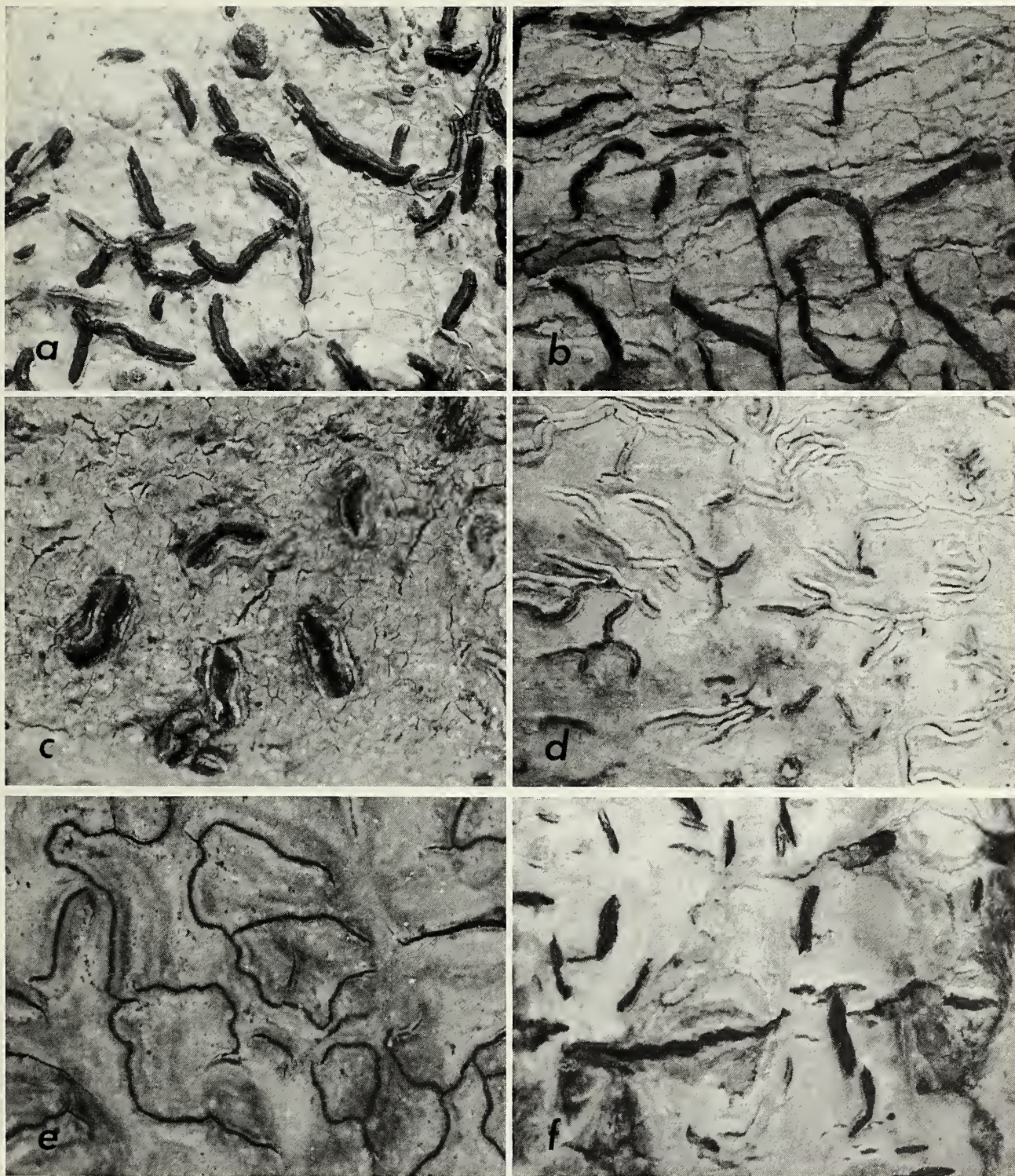


PLATE 2.—Species of *Graphis*: a, *G. dussii* (Hale 35443); b, *G. elegans* (Hale 35476); c, *G. flexibilis* (Imshaug 33360); d, *G. glaucescens* (Imshaug 33313A); e, *G. grammitis* (Hale 38005); f, *G. humilis* (Hale 35698).

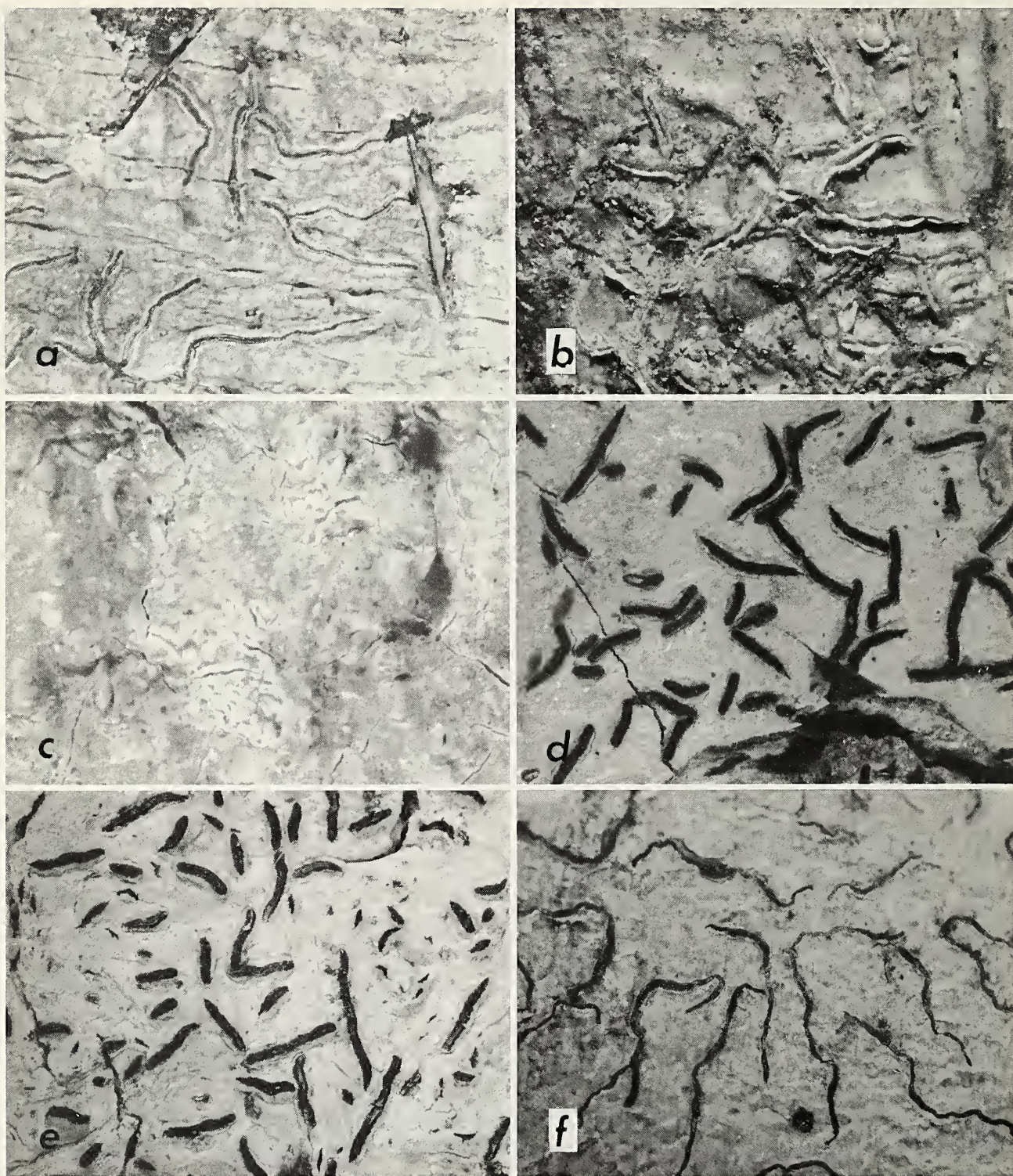


PLATE 3.—Species of *Graphis*: a, *G. imshaugii* (Imshaug 32724 in MSC); b, *G. insidiosa* (Hale 35313); c, *G. isidiifera* (Hale 35179); d, *G. leptocarpa* (Imshaug 33109A); e, *G. librata* (Wirth 538); f, *G. longula* (Hale 35225).

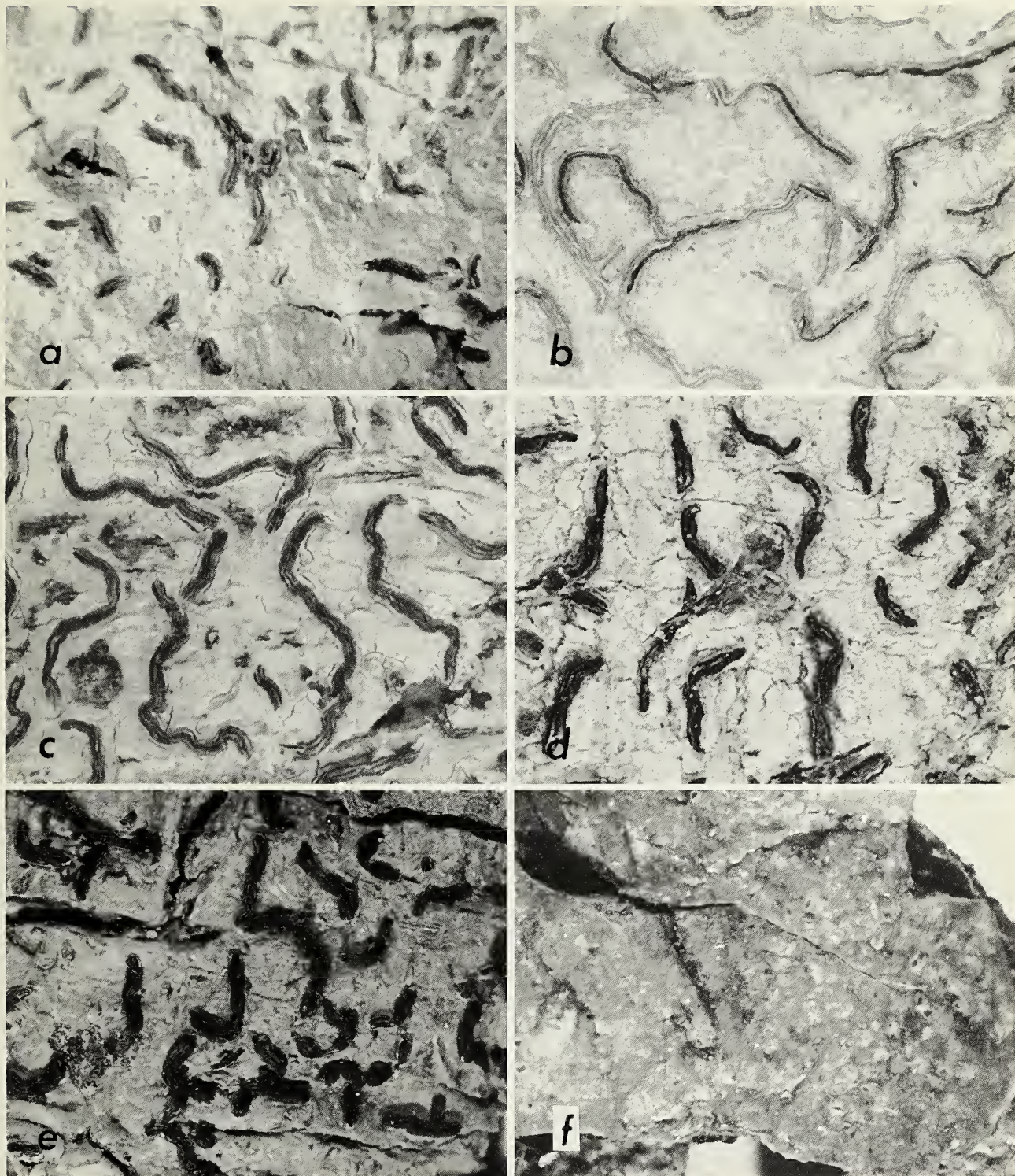


PLATE 4.—Species of *Graphis*: a, *G. lumbricina* (Hale 35240); b, *G. olivacea* (Hale 37988); c, *G. rigidula* (Imshaug 32777A); d, *G. rimulosa* (Hale 35699); e, *G. subelegans* (Hale 35546); f, *G. subnitidula* (Hale 37676).

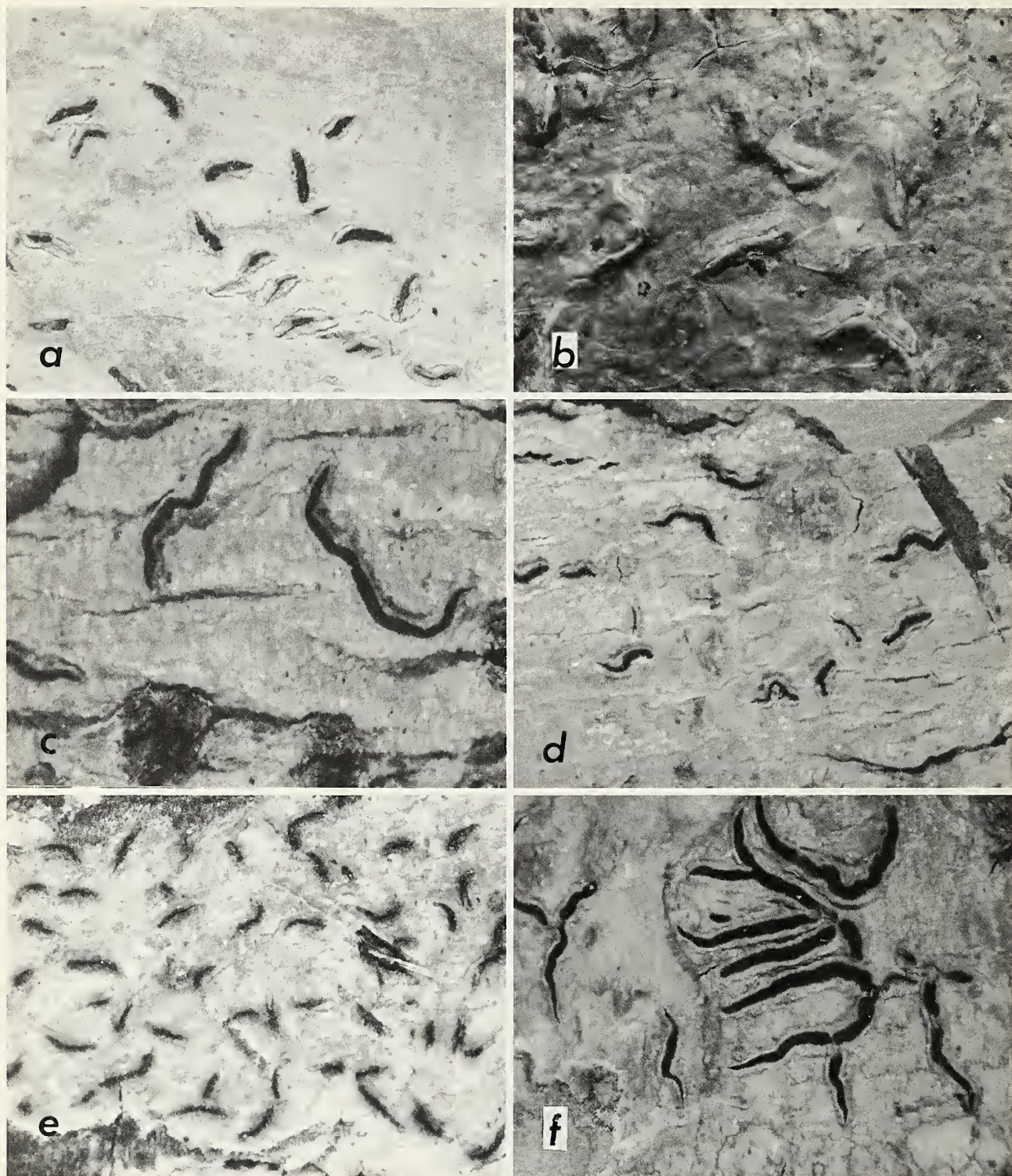


PLATE 5.—Species of *Graphis* and *Phaeographis*: a, *G. tachygrapha* (Imshaug 32862A); b, *G. triticea* (Hale 35324); c, *G. turgidula* (Wirth 544b); d, *P. albida* (Hale 35453); e, *P. arthonioides* (Imshaug 33128); f, *P. exaltata* (Hale 35301).

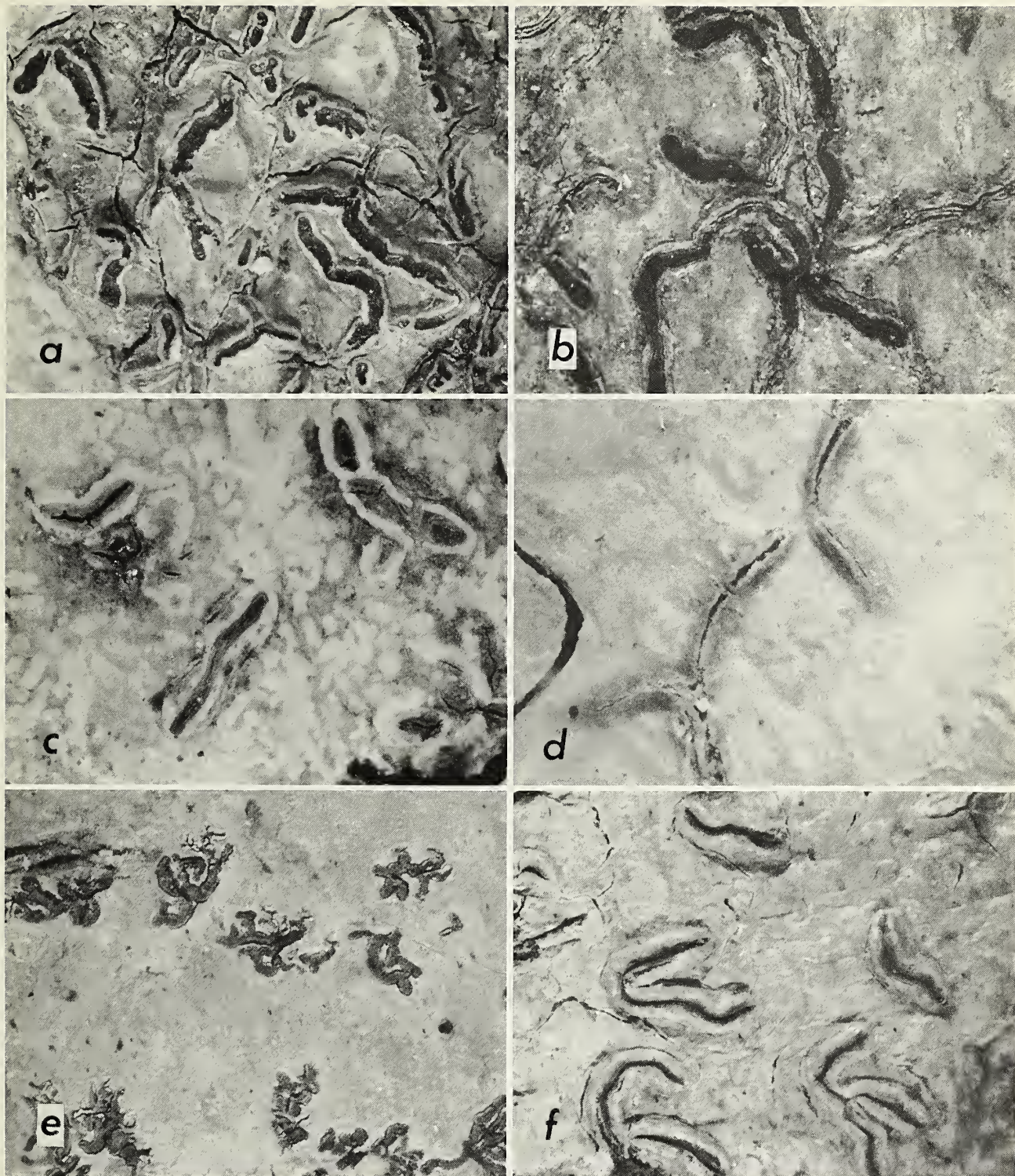


PLATE 6.—Species of *Phaeographis* and *Graphina*: a, *P. exaltata* (Hale 35321); b, *P. haematites* (Hale 38013); c, *P. mordenii* (Hale 35071); d, *P. rosea* (Elliott in BM); e, *P. subtigrida* (Wirth 444); f, *G. acharii* (Hale 35555).

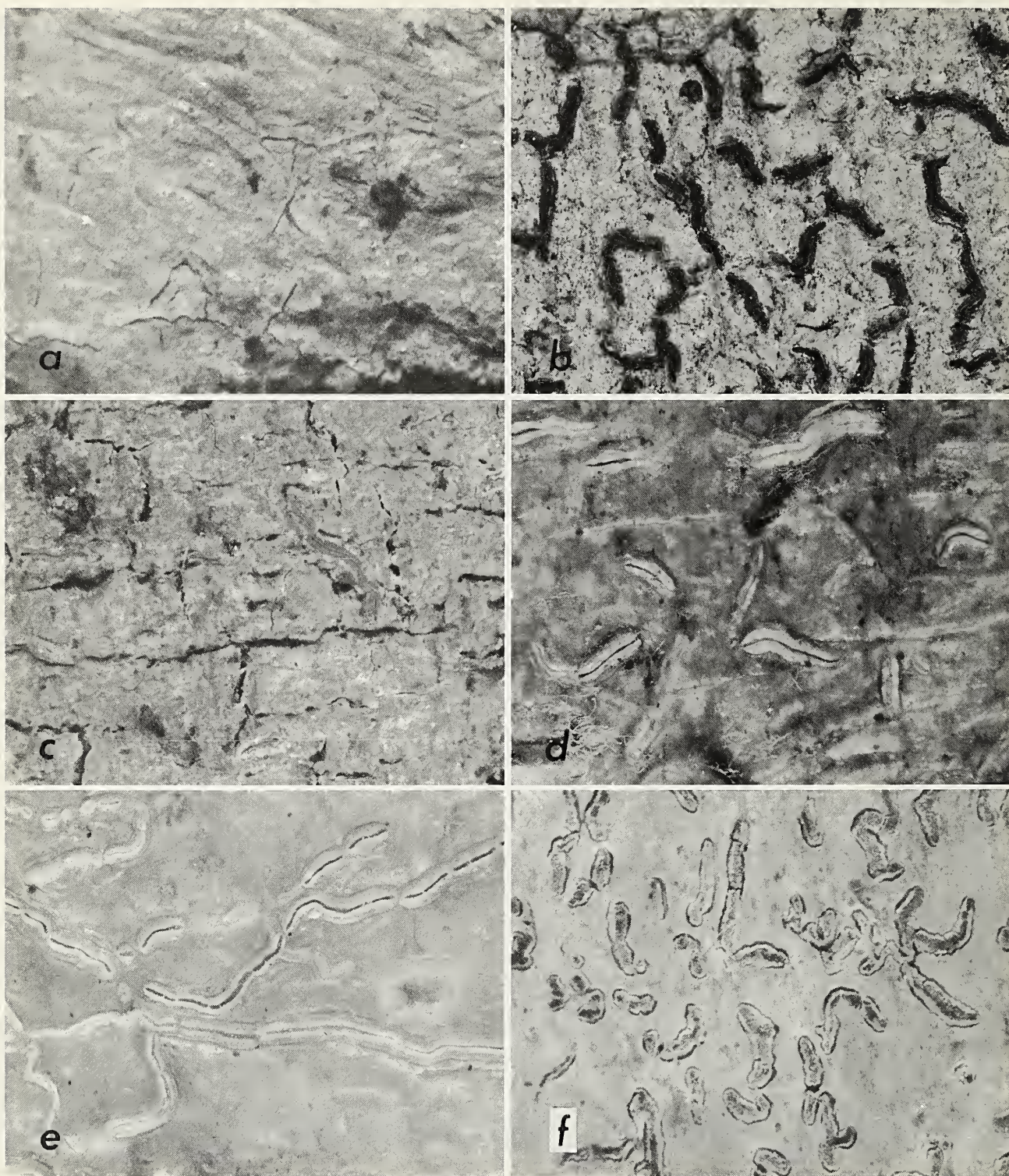


PLATE 7.—Species of *Graphina*: a, *G. adscribens* (Wirth 519); b, *G. antillarum* (Hale 35745); c, *G. carneoviridis* (Hale 37642); d, *G. chlorocarpa* (Hale 35129); e, *G. colliculosa* (Hale 35175); f, *G. collospora* (Wirth 520).

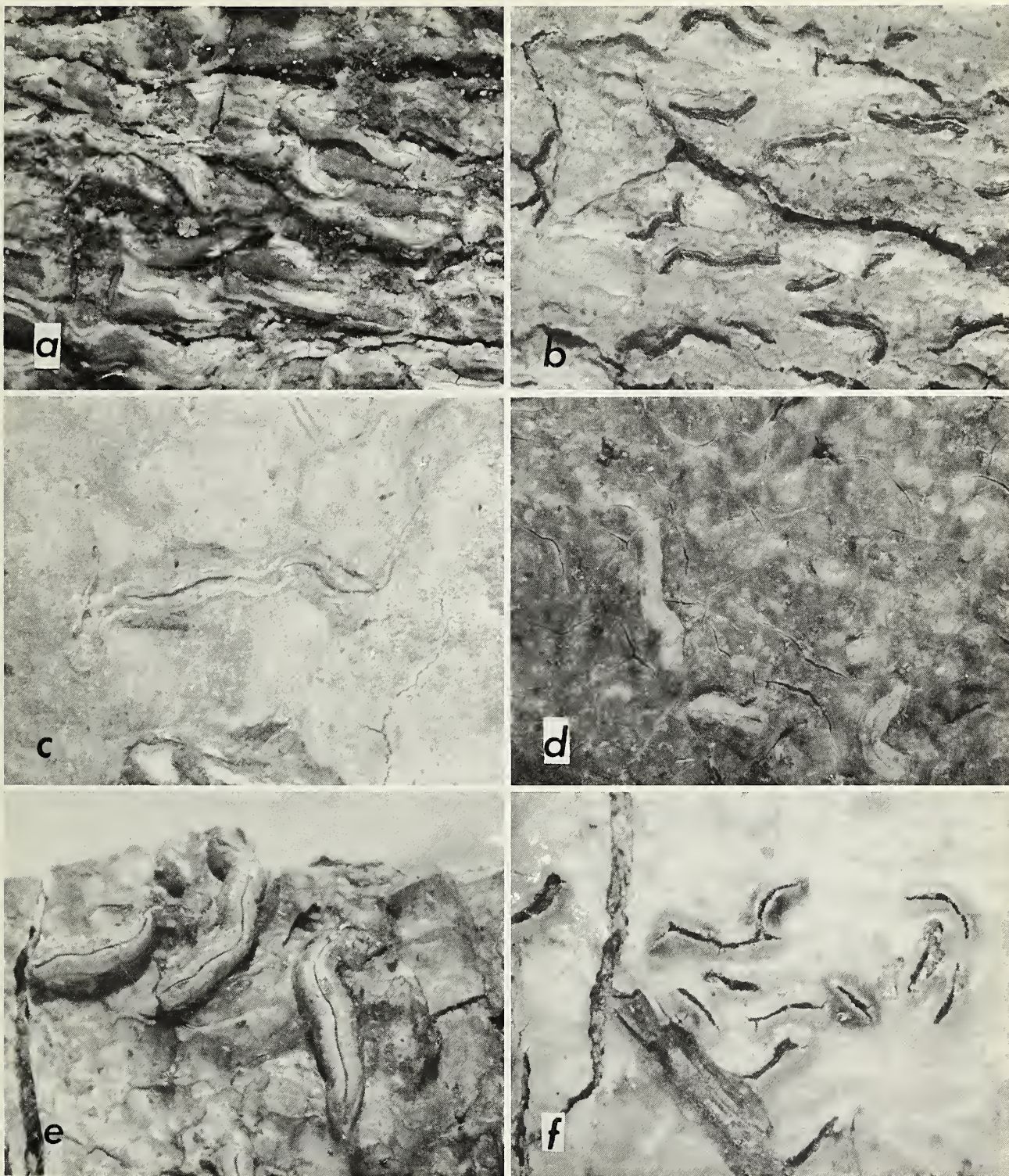


PLATE 8.—Species of *Graphina*: *a*, *G. columbina* (Wirth 446); *b*, *G. dimidiata* (Hale 35697); *c*, *G. dispersa* (Hale 38090); *d*, *G. frumentaria* (Hale 35242); *e*, *G. illinata* (Hale 35284); *f*, *G. incrustans* (Wirth 465).

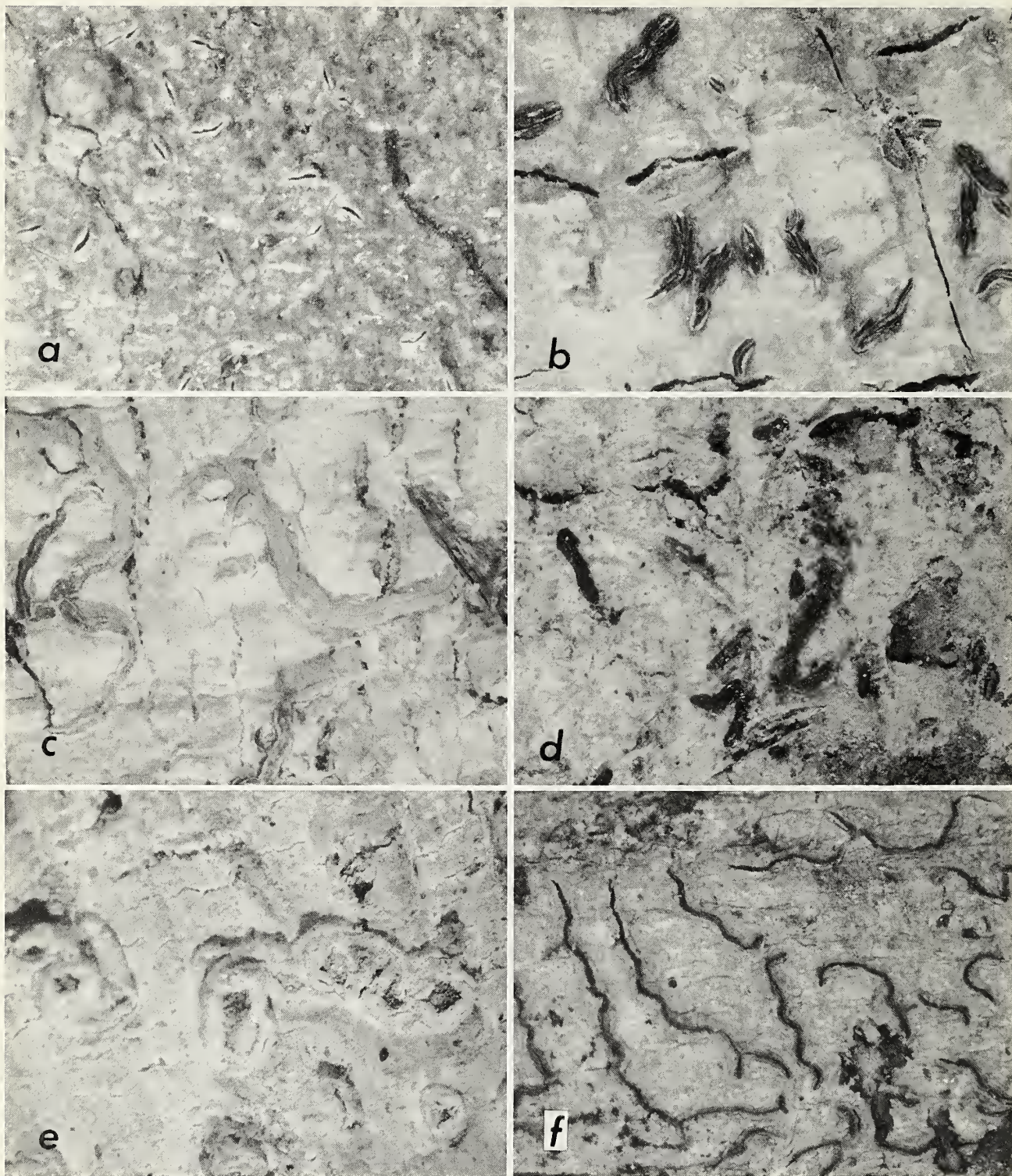


PLATE 9.—Species of *Graphina*: a, *G. insculpta* (Hale 37819); b, *G. macella* (Hale 35723); c, *G. marcescens* (Hale 35312); d, *G. nuda* (Hale 35119); e, *G. platyleuca* (Hale 37955); f, *G. plurispora* (Imshaug 37724A).

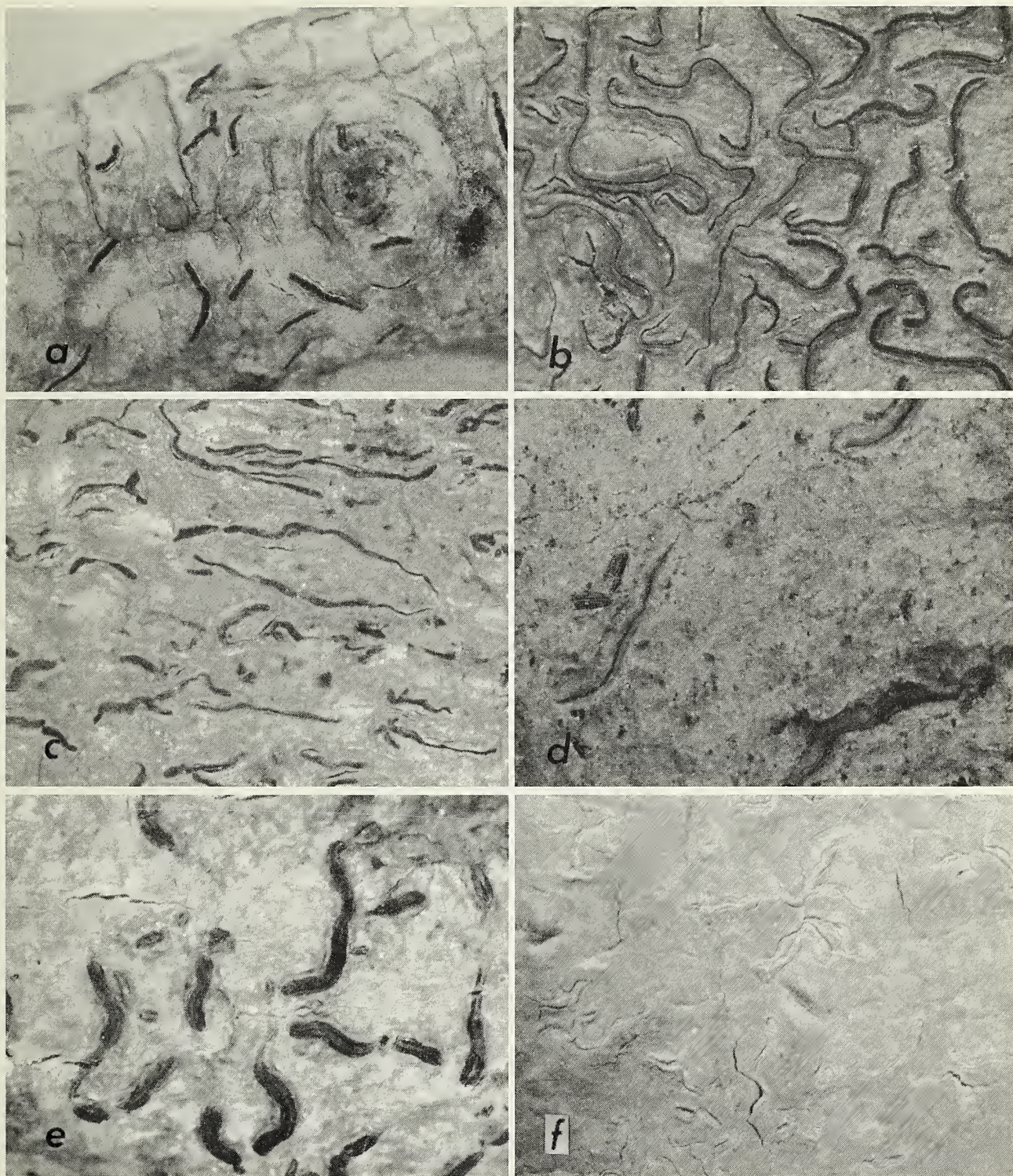


PLATE 10.—Species of *Graphina*: a, *G. pseudoanaloga* (Hale 35283); b, *G. rufopallida* (Elliott 1852); c, *G. suberythrella* (Imshaug 32699); d, *G. triphoroides* (Hale 35161); e, *G. vestitoides* (Imshaug 32859A); f, *G. virginea* (Wirth 547).

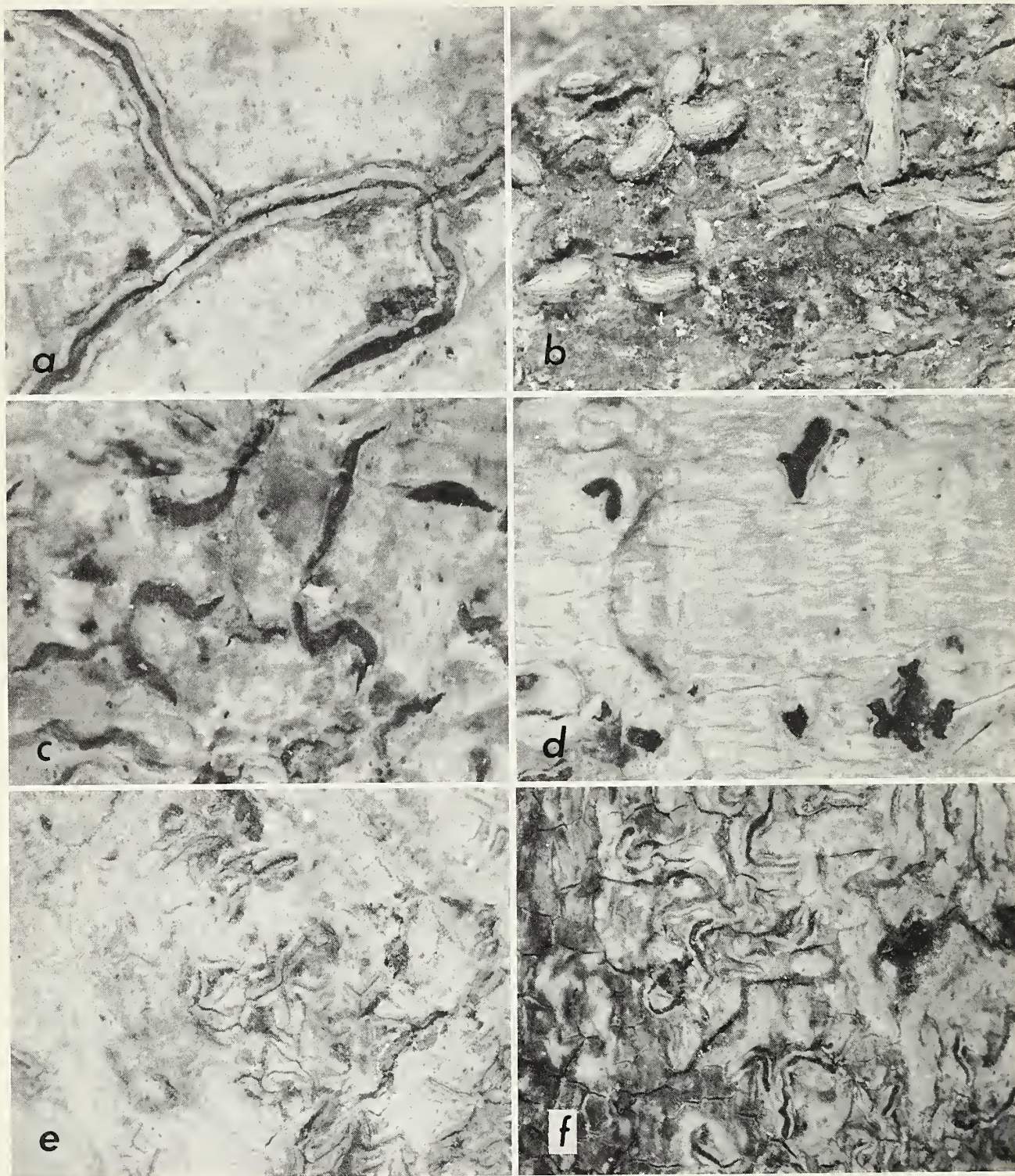


PLATE 11.—Species of *Phaeographina*: a, *P. atrovermicularis* (Hale 35278); b, *P. caesiopruinosa* (Imshaug 32713); c, *P. coriaria* (Hale 35378); d, *P. difformis* (Imshaug 32913A); e, *P. elliottii* (Elliott 1338 in TUR); f, *P. oscitans* (Hale 35131).

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